

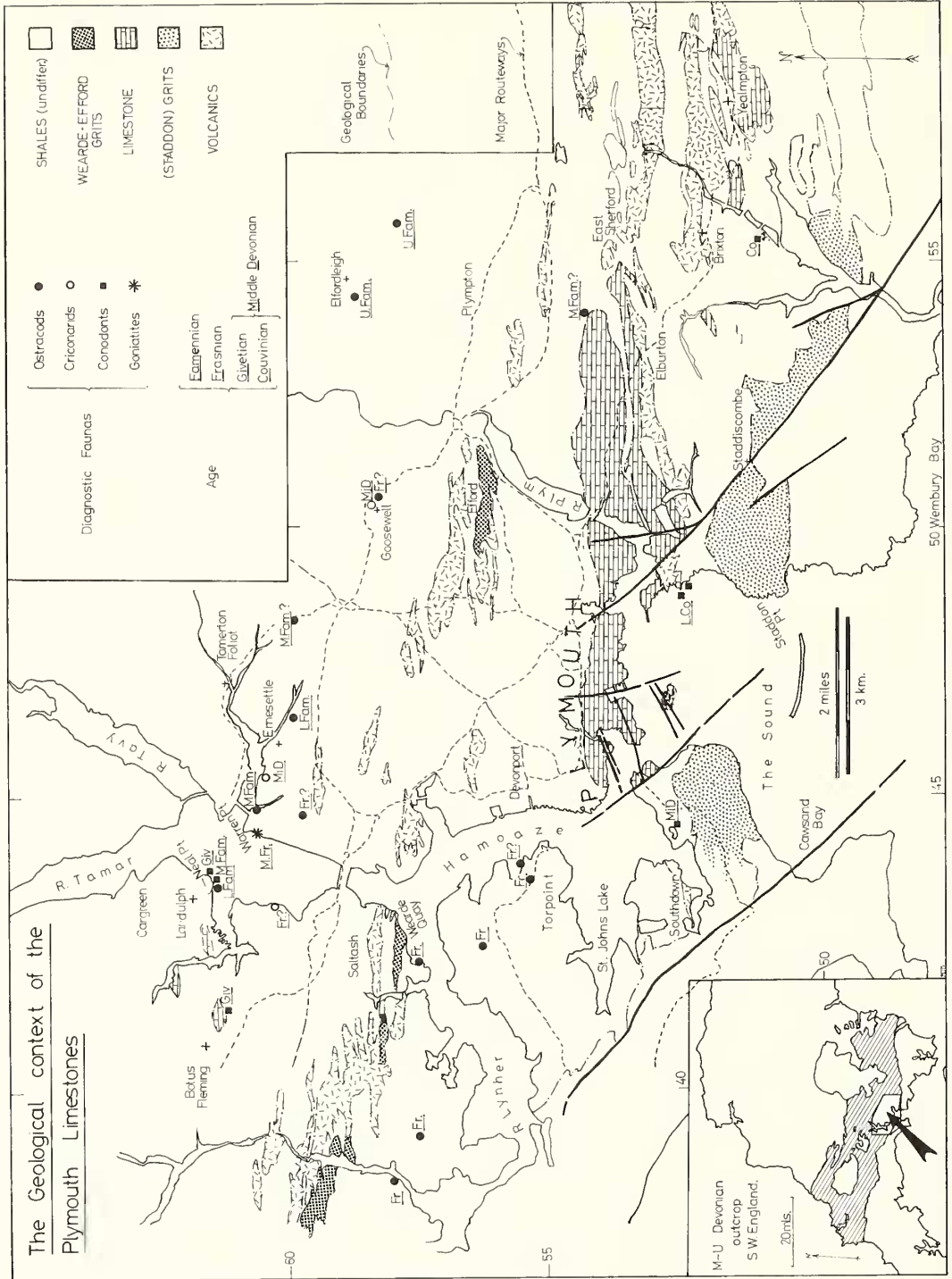
# THE CONODONT BIOSTRATIGRAPHY OF THE DEVONIAN PLYMOUTH LIMESTONE, SOUTH DEVON

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**ABSTRACT.** Conodont faunas from the Plymouth Limestone are indicative of levels ranging from the Middle Devonian *patulus* Zone to the Upper Devonian *crepida* Zone. The conodont faunas are described and compared with European counterparts, with which correlations are proposed. Although there are anomalies in some distributions, the conodonts have provided a tool for the dating and correlation of disjunct sections of Plymouth Limestone, and have enabled the elucidation of stratigraphical, palaeoenvironmental and structural aspects of the carbonates. Thus: the history of the Limestone began in the early Eifelian but was interrupted by a mid to late Eifelian volcanic episode; this was followed by the growth of a carbonate platform during the late Eifelian-mid Givetian. A late Givetian to early Frasnian carbonate maximum, which involved facies differentiation (more restricted environments are recognized in the east and south-east), was followed by an interval of widespread deepening (Lower *asymmetricus* Zone times). Deposition of massive Frasnian limestones ensued prior to local, mid Frasnian crevassing and further foundering in the early Famennian. The area is inferred to have stood as a topographic high within the late Devonian sea. The Limestone mass has been overfolded in the east but no inverted limb is recognized in the western outcrop.

IN western South Devon, the oldest Devonian rocks, the Dartmouth Slates, are comparable with the non-marine Old Red Sandstone (Dineley 1966) and represent a relatively uniform continental phase preceding the marine sedimentation of the overlying Meadfoot Beds. The latter, dominantly argillaceous rocks, are succeeded to the north by the Staddon Grits and the Jennycliff Slates (see also Orchard 1977).

The Plymouth Limestone occupies a position to the north of the aforementioned Slates. The present outcrop, in all about two-and-a-half square kilometres, borders the Sound on three sides. On the south-east side, the basal beds of the Limestone are seen at Dunstone Point (SX489526) but on the Cornish coast south of Cremyll (see text-fig. 3), the massive dolomitized limestones on the north of the Lower Devonian(?) argillites are Upper Devonian in age, and a large intervening fault is inferred. The westernmost outcrop is at present seen at Mutton Cove (SX453540). Further westward, on the borders of the Hamaoze, there are a variety of igneous rocks, purple and green slates, and the enigmatic Wearde Grit (see text-fig. 1; Ussher 1907, pp. 82-90), but these are mostly undated and relationships are obscure. Further to the north-west, shales and limestone turbidites are seen at Botus Fleming (SX409612) and at Neal Point (SX436613). The northern margin of the Limestone lies within the City of Plymouth and is not generally visible, although long ago Hennah (1822, p. 8) gave details of its course; there are also borehole records (see Ussher 1907, pp. 59-61). Purple ostracod-bearing slates are known to the north of the Limestone and Gooday (1975) has dated some of these (see text-fig. 1). The Efford Grit occurs within this slate belt and is regarded as an equivalent of the development at Wearde Quay. Eastward, the Limestone appears to pass laterally into shales, although these are



TEXT-FIG. 1. Geological setting of the Plymouth Limestone. In part based on the Geological Survey one inch maps nos. 348, 349. Ostracode ages after Gooday 1975. For location of the conodont faunas within the Plymouth Limestone see Figs. 3-5.

sometimes calcareous and locally massive limestones occur, as for example in Venn Quarry, Brixton (SX557524).

#### CONODONT SUCCESSION IN THE PLYMOUTH LIMESTONE

Fifteen distinctive conodont faunas (hereafter Faunas 1-15) are recognized in the Plymouth area. The Faunas come from tectonically isolated limestone sections in which only a few of the associations are seen in actual succession, but the following account is nevertheless judged to be arranged in ascending stratigraphical order. Conclusions regarding the relationship of the Faunas to zonal schemes derived from successions in Germany and Belgium is summarized in text-fig. 2. The gaps between the Faunas is in part a reflection of the structural complexity of the Limestone, in part they are due to unfavourable carbonate facies, and in the Upper Devonian, the latest is thought to be due to a non-sequence within the Limestone. Full details of the conodont faunas are given in Tables 1-2.

In the following account, abbreviations used are: *A.* = *Ancyrodella*, *I.* = *Icriodus*, *Pa.* = *Palmatolepis*, *Po.* = *Polygnathus*, *S.* = *Spathognathodus*. Figures in parentheses refer to sample numbers which are located in text-figs. 3-5, and to grid references, all of which bear the prefix SX.

##### *Fauna 1* (MB23, Dunstone Point SX48855261):

Here, the first substantial carbonate development in the Plymouth area has yielded *I. corniger*, and *I. retrodepressus*. The former lends its name to the Lower Eifelian *corniger* Zone in Germany, where it ranges throughout that Zone and into the overlying *bidentatus* Zone (Ziegler 1971, chart 2). A comparable interval is recognized in Belgium although there the Zone is regarded as embracing forms, referred to *I. aff. corniger* by Bultynck (1972), in beds (Em3) older than the Eifelian. The broader interpretation of the *corniger* Zone has been followed during recent revision of the German conodont successions (Weddige and Ziegler 1977), which has laid more emphasis on the sequence of polygnathid species (as originally worked out in the New York Devonian by Klapper 1971) for zonation of the Eifelian, although such forms are conspicuously absent in Fauna 1. Nevertheless, the *corniger* Zone is superseded by the Zone of *Po. costatus patulus*, with which it approximates. *I. retrodepressus* is known from within the upper part of the *patulus* Zone where it dominates faunas in the interval between the disappearance of *Po. serotinus* and the incoming of 'typical' *I. corniger* (Weddige and Ziegler 1977, fig. 1, p. 75). Bultynck (1972) recorded *I. retrodepressus* from the middle part of the *corniger* Zone in Belgium, specifically in the upper parts of Co1c into the lower part of Co2b.

*Fauna 2* (RW39, Richmond Walk): At the southern end of Richmond Walk (text-fig. 4a/39; SX45915408), a small exposure in limestones similar to those at Dunstone Point yield what is regarded as a slightly younger association: *I. corniger*, *I. n.sp. A*, and a single polygnathid referred to *Po. aff. porcillus* Stauffer. The latter is superficially similar to small specimens of *Po. linguiformis* and may relate the latter to the Eifelian *Po. angustipennatus*, a relationship suggested by Bultynck (1970, p. 122, fig. 16). The author has seen similar forms in a collection from the *Zwischenschichten* (of Blauer Bruch, Germany) which is referred to the upper Eifelian *kockelianus* Zone.

| GERMANY         |              |             |                      | BELGIUM |          |                         |                       | S. W. Devon       |               |                 |          |
|-----------------|--------------|-------------|----------------------|---------|----------|-------------------------|-----------------------|-------------------|---------------|-----------------|----------|
| (pars)          |              |             |                      |         |          |                         | mgm                   |                   |               |                 |          |
| UPPER DEVONIAN  | Cheiloc.     | U           | crepida              | FAMENN. |          | U                       | 29                    |                   |               |                 |          |
|                 |              | M           |                      |         |          | 28                      |                       |                   |               |                 |          |
|                 |              | L           |                      |         |          | 27                      |                       |                   |               |                 |          |
|                 | Manticoceras | U           | Pa. triangularis     |         |          | U                       | 26                    |                   | Fauna 15      |                 |          |
|                 |              | M           |                      |         |          | 25                      |                       |                   |               |                 |          |
|                 |              | L           | 24                   |         |          |                         |                       |                   |               |                 |          |
|                 |              | U           | gigas                |         |          | F3b                     | 23                    |                   | U. gigas s.l. |                 |          |
|                 |              | M           |                      |         |          | 22                      | Ag. triangularis s.l. |                   | Fauna 14      |                 |          |
|                 |              | L           |                      |         |          | 22                      |                       |                   |               |                 |          |
|                 |              |             | Ag. triangularis     |         |          | F2j                     | 22                    |                   |               |                 |          |
|                 |              |             | U                    |         |          | asymmetricus            | F2ih<br>F2g<br>F2f    |                   | 21            | An. curvatus    | Fauna 13 |
|                 |              |             | M                    |         |          |                         | 20                    |                   | An. gigas     | Fauna 12        |          |
|                 |              |             | L                    |         |          |                         | 19                    |                   |               |                 |          |
|                 |              |             | Lm                   |         |          | hermanni-<br>-cristatus | F2<br>a-c             |                   | 18            | An. rotundiloba | Fauna 11 |
|                 |              |             | U                    |         |          |                         | 17                    |                   | insitus       | Fauna 10        |          |
| L               | 17           |             |                      |         |          |                         |                       |                   |               |                 |          |
| MIDDLE DEVONIAN | Maenioceras  |             | U                    | varcus  | GIVETIAN |                         | varcus                | 16                | Fauna 9       |                 |          |
|                 |              |             | M                    |         |          |                         |                       | 16                | Fauna 8       |                 |          |
|                 |              | L           | 15                   |         |          |                         |                       | Fauna 7           |               |                 |          |
|                 |              | U           | 14                   |         |          |                         |                       |                   |               |                 |          |
|                 | EIFELIAN     | kockelianus | australis            | U       |          |                         | 14                    | obliquimarginatus | Fauna 6       |                 |          |
|                 |              |             |                      | M       |          |                         | 13                    |                   |               |                 |          |
|                 |              |             |                      | L       |          |                         | 13                    |                   |               |                 |          |
|                 |              | bidentatus  | costatus<br>costatus | U       |          |                         | 12                    | kockelianus       | Fauna 5       |                 |          |
|                 |              |             |                      | M       |          |                         | 11                    | Fauna 4           |               |                 |          |
|                 |              | corniger    | costatus<br>patulus  | U       |          |                         | 10                    |                   | Fauna 3       |                 |          |
|                 |              |             |                      | M       |          |                         | 9                     |                   |               |                 |          |
|                 |              | EMSIAN      |                      |         |          |                         | U                     | 8                 | ?             | Fauna 2         |          |
|                 |              |             |                      |         |          |                         | M                     | 7                 |               |                 |          |
|                 |              |             |                      |         |          |                         | L                     | 6                 |               |                 |          |
|                 |              |             |                      |         |          |                         | U                     | 5                 | corniger      | Fauna 1         |          |
|                 |              |             | M                    | 4       |          |                         |                       |                   |               |                 |          |
|                 |              |             | L                    | 3       |          |                         |                       |                   |               |                 |          |
|                 |              |             | U                    | 2       |          |                         |                       |                   |               |                 |          |
|                 |              | M           | 1                    |         |          |                         |                       |                   |               |                 |          |

TEXT-FIG. 2. Middle and Upper (in part) Devonian conodont zonation and succession in Germany and Belgium, and the age of Faunas 1-15 from Plymouth. European correlation and division based principally on Wittekindt 1966, Bultynck 1970, 1972, 1975, Ziegler 1971, Bouckaert *et al.* 1972, Carls *et al.* 1972, Buggisch and Clausen 1972, Mouraviëff and Bouckaert 1973, Bouckaert and Strel 1974, Ziegler *et al.* 1976, Weddige and Ziegler 1977, House and Ziegler 1977.

















Stauffer (1940) described a similar polygnathid from above the Cedar Valley Limestone (admixed fauna) of Austin, Minnesota. The presence of *I. corniger* in Richmond Walk suggests that Fauna 2 is no younger than mid Eifelian in age.

*Fauna 3* (FR1-7, Faraday Road): The oldest limestones in the north-eastern outcrop are seen on the south side of Farady Road (text-fig. 5*b*; SX49775422) to the north of Cattedown. These are flaggy crinoidal limestones bearing rather sparse faunas which include *Po. pseudofoliatius*, rare *S. bidentatus* and common simple cones. *Po. pseudofoliatius* characterizes an interval identified by several authors within the late Eifelian (e.g. Klapper 1971, Perry *et al.* 1974, Telford 1975), and regarded by Klapper (1977, p. 47) as equivalent to the *australis* or *kockelianus* Zone. In Belgium too *Po. pseudofoliatius* occurs most frequently in the upper Couvinian (Bultynck, *in* Bouckaert and Streef 1974). The form is known to range as high as the Lower *varcus* Subzone (Ziegler *et al.* 1976). The appearance of *S. bidentatus* was regarded as defining the base of the mid Eifelian *bidentatus* Zone in Germany, but in Belgium the form is not known before the late Couvinian (Co2d). In terms of the revised zonal nomenclature, *S. bidentatus* appears a little above the base of the *costatus costatus* Zone (in Hercynian facies only: Weddige and Ziegler 1977, p. 75). Fauna 3 is regarded as no younger than late Eifelian in age, since it lies below strata bearing *Po. angustipennatus* s.l. (Fauna 4).

*Fauna 4* (FR8-9, Faraday Road; L1d, Laira Bridge; DI5, 6, Drake's Island): In Faraday Road, in the midst of the tuffs and argillites which follow the limestones bearing Fauna 3, a development of stromatoporoid-bearing limestone (*c.* 2.5 m thick) has yielded the long-ranging *Po. linguiformis linguiformis* (= gamma morphotype, see below) and a single *Po. angustipennatus* s.l., in addition to abundant simple cones. The same limestone development is exposed in the Laira Bridge cut (text-fig. 5/1*d*; SX50015430). On Drake's Island, bedded limestones on the west of the Island (text-fig. 4*d*/DI6; SX46705296) and a limestone raft (text-fig. 4*d*/DI5; SX46735291) within adjacent tuffs have also each yielded a single specimen of *Po. angustipennatus* s.l.; Ziegler (1973) regards the range of this species as no younger than mid-late Eifelian in age.

Beneath the limestone at Laira, a fossil horizon (text-fig. 5*b*/1*a*; SX50005431) within grey-green slates includes *Pleurodictyum* and trilobites which Burton (1972) considers may date from the Middle-Upper Emsian or possibly the lowest Eifelian. However, this horizon has not been traced in Faraday Road, and I suspect that there is some structural dislocation at Laira.

*Fauna 5* (FR13-14, Faraday Road; PS01-2, Plymouth Power Station = Princerock Quarry; TH44, Teats Hill Quarry; ?CR3, Cattewater Road): A belt of dark, argillaceous limestone seen in northern Princerock and separated from the limestones bearing Fauna 4 in Faraday Road by some 17 m of tuffs and shale, strike westward and are seen again on the northern edge of Teats Hill Quarry in Coxside (SX486541). Conodont faunas from these carbonates are larger and more diverse than Faunas 1-4, although they do have several species in common. For example, *Po. pseudofoliatius*, *Po. l. linguiformis*, and the simple cones occur frequently and *S. bidentatus* reappears in a fauna from the northern outcrop in Princerock Quarry (text-fig. 5*b*/O2;

SX49845417) and occurs also in Teats Hill Quarry (text-fig. 5c/44; SX48635406). In both the latter and in the Faraday Road–Princerock Quarry section, *I. regularicrescens* and another icriodid similar to *I. difficilis* join the aforementioned species.

*I. regularicrescens* is particularly characteristic of Upper Couvinian levels in Belgium (Bultynck 1972: upper part of Co2c and Co2d); the species has been found as high as the Lower *varcus* Subzone by Ziegler *et al.* (1976, table 12). In Teats Hill Quarry, *Po. xylus ensensis* is an additional associate in the faunas. This polygnathid is known from unspecified Eifelian levels and as high as the Middle *varcus* Subzone (Ziegler *et al.* 1976). In Cattewater Road (text-fig. 5b/CR3; SX4995425), a limestone on strike to those bearing Fauna 5 in Faraday Road, has yielded the distinctive ozarkodiniform element of the multielement *Pandorinellina expansa*. This species is known from as high as the late Eifelian in Canada (*Po. pseudofoliatus*-*Po. aff. eiflius* Fauna, Uyeno and Mason 1975, text-fig. 2), but also in rather older beds in the Yukon (Perry *et al.* 1974), Nevada (Klapper 1977), in Eastern Australia (Fordham 1976, tables 1, 2), and in Germany (Weddige and Ziegler 1977). Fauna 5 is judged to represent a late Eifelian interval.

*Fauna 6* (PS3, 4, Princerock Quarry; CQ10, Cattedown Quarry; GW20, 16, Gasworks Quarry; ?TH46–49, Teats Hill Quarry and foreshore; D12–13, Drake's Island; NP2, 13, 15, Neal Point): Princerock Quarry is principally developed in dark limestones which have yielded the following association: *I. obliquimarginatus*, *Po. linguiformis* ?epsilon morphotype, *Po. aff. variabilis* and *S. bidentatus*. In Germany, *I. obliquimarginatus* is found in the zone of that name and ranges as high as the Middle *varcus* Subzone (Ziegler *et al.* 1976, p. 113). In Belgium, the species is found within the highest Couvinian and in zones Gia and Gib (Bultynck, *in* Bouckaert and Strel 1974). Relatively small elements (?juveniles) referred with question to the epsilon morphotype of *Po. linguiformis* are characteristic of this Fauna. These have not been found in younger faunas associated with typical, larger representatives of the epsilon morphotype, and they may consequently prove to be of some stratigraphic value. *Po. aff. variabilis* is similar to the species described previously from Germany (Bischoff and Ziegler 1957, Wittekindt 1966) and Indiana (Orr 1971) from different levels in the late Middle and early Upper Devonian, but it is a narrower concept than *Po. variabilis* and is not found outside Fauna 6. The latest recorded range of *S. bidentatus* is the low Givetian both in Belgium (Bultynck, *in* Bouckaert and Strel 1974) and Germany (the Lower *obliquimarginatus* Zone, Ziegler 1971, chart 2). The Princerock faunas are regarded as low Givetian, *obliquimarginatus* Zone in age.

Towards the west, in the Gasworks (Esso) Quarry (text-fig. 5a/20; SX49295389), a more abundant fauna includes, in addition to most of the aforementioned Princerock Quarry association, *S. brevis*, *Po. latus* and representatives of the *I. expansus* group. *S. brevis* has previously been regarded as no older than the *varcus* Zone (Wittekindt 1966, table 1, p. 627; Ziegler 1971, p. 258), although this is not the first record of the form in faunas which lack the *varcus* morphotype which marks the base of that Zone, *Po. timorensis* (see below). *Po. latus* was originally described from the *eiflia* Zone of Wittekindt (1966, table 1) = Lower *obliquimarginatus* Zone, where it was not common. Wittekindt found ten specimens, and the only subsequent records are those of Boersma 1973 (table 2, p. 352: 1–3 specimens from the A member of the



Compte Formation) in the Spanish Pyrenees, and Bultynck (*in* Bouckaert and Streel 1974, E, p. 15: a single specimen from sample 57, Menil) in Belgium. These subsequent records have not been accompanied by illustration of the species, but they are consistent with a range in the lower part of the Givetian. This, and the similarity between the Gasworks Quarry fauna and that from Princerock Quarry, suggests that the former might also be referred to the *obliquimarginatus* Zone (in the sense of Ziegler 1971). If this were accepted, then *S. brevis* would be regarded as older than the *varcus* Zone, as would two rather anomalous records in the literature: the association of *S. brevis*, *S. bipennatus*, *Po. pseudofoliatus* and *Po. eiflius* from the Timor Limestone of New South Wales (Pedder *et al.* 1970, pp. 263, 265) and *S. brevis* in association with *Po. parawebbi* in Willow Creek, Nevada (Ziegler *et al.* 1976, pp. 113, 121, table 6). At the top end of its range, *S. brevis* has been found in the Middle *asymmetricus* Zone (Bischoff and Ziegler 1957, table 4).

In east Cornwall, some limestones from Neal Point (SX436613) are also thought to date from the *obliquimarginatus* Zone (see also Matthews 1962). There (text-fig. 5f/NP2; SX43556122), the author has found two specimens of *Po. latus* and, in a second sample (NP15; SX43596125), a single *S. bipennatus*. The latter species has been recorded from the *obliquimarginatus* Zone in Germany (Bischoff and Ziegler 1957) and Belgium (*in* Bouckaert and Streel 1974). The long ranging *I. difficilis* (see Ziegler *et al.* 1976, tables 1–6, 13–15) also occurs at Neal Point.

The massive limestones in the south of Teats Hill Quarry (text-fig. 5c/47–49; SX48585402) have yielded low diversity faunas dominated by icriodids which are referred to the *I. expansus* group. Identical icriodids occur in the eastern-most limestones on Drake's Island (text-fig. 4d/1–3; SX46855292). These icriodids are very similar to those in the Gasworks Quarry fauna (GW20), with which they are therefore tentatively correlated. The late growth stages of these icriodids resemble *I. arkonensis*, a form recorded from the Givetian of North America (Klapper, *in* Ziegler 1975), but for reasons discussed below they are referred to a generalized *I. expansus* group.

*Fauna 7* (RW5–9, Richmond Walk): The northern horizons of Richmond Walk (text-fig. 4a/5–9; SX46085441) yield faunas in which *S. brevis* is associated with *Po. timorensis* (including the juvenile *Po. rhenanus*), the long ranging *Po. l. linguiformis* and abundant simple cones. This association is consistent with a Lower *varcus* Subzone age (Ziegler *et al.* 1976).

*Fauna 8* (RW10–13, 25–28, ?41–44, Richmond Walk; MC32, Mutton Cove; DM50, 51, Deadman's Bay, Coxside; ?H2, West Hoe; BF1–3, Botus Fleming): Immediately overlying fauna 7 in Richmond Walk are limestones which include, in addition to those species in the preceding Fauna, *Po. ansatus*, *I. latericrescens latericrescens*, and the ?delta morphotype of *Po. linguiformis*. The appearance of *Po. ansatus* defines the base of the Middle *varcus* Subzone (Ziegler *et al.* 1976) while the delta morphotype also characterises this interval (*op. cit.* tables 10–13). The record of *I. l. latericrescens* is of interest since although the species occurs throughout the Givetian in eastern North America, in Europe it occurs infrequently, and only within a short interval about the Lower-Middle *varcus* Subzonal boundary (Ziegler *et al.* 1976, tables 10, 12). In Richmond Walk, the icriodid occurs within a two-metre interval. A composite

fauna from these beds in Richmond Walk originally yielded rare specimens of *Po.* aff. *latifossatus* which might be the precursor of the species which characterizes the Upper *varcus* Subzone. Forms referred to '*Polygnathellus*' and '*Bryantodus*' occur sporadically in Richmond Walk but they are poorly known; similar elements recorded by Bischoff and Ziegler (1957) appear to have a restricted range about this level. *Po. xylus ensensis* (one specimen) is known from the thick bioclastic horizons (text-fig. 4a/28; SX46055439) in Richmond Walk, and this supports an age no younger than Middle *varcus* Subzone for these lower bioclastic limestones. The only conodonts found in the southern (higher beds) in Richmond Walk (e.g. text-fig. 4a/44; SX45895409) are poorly preserved polygnathids indicative of a non-specific *varcus* Zone age.

Other faunas referred to Fauna 8 include that from red dolomitized limestone in Mutton Cove (text-fig. 5d/32; SX45305401) where the epsilon morphotype of *Po. linguiformis* is common, and another from near Botus Fleming (text-fig. 5f/BF1-3; SX40966115) where *Po. ansatus* is associated with a single specimen of the delta morphotype. Ussher (1907, p. 74) regarded the limestones in the vicinity of Botus Fleming as Upper Devonian in age.

The southern horizons of Coxside, in Deadman's Bay (text-fig. 5c/50-51; SX48785383) and much of the massive limestone on the Hoe foreshore (e.g. text-fig. 5e/2; SX47675380) are judged to be contemporary developments within the central parts of the carbonate complex. These bear rather fragmented conodont faunas similar to those from the southern beds of Richmond Walk.

*Fauna 9* (MW36): A fauna from Mount Wise (text-fig. 5d/36; SX45555404) is relatively abundant and includes some of the better preserved of the Plymouth conodonts. Of particular note is the presence of *Po. tuberculatus* and relatively common *Po. l. mucronatus*, two species which characterized the *transversus* Zone of Wittekindt (1966). *Po. tuberculatus* has previously been reported from the Genundewah Limestone of New York (Hinde 1879, Bryant 1921), the Lower Albany Shale of Indiana (Huddle 1934), and from the Himalayas (Gupta 1975a, b). These faunas have been assigned to the *hermanni-cristatus* or Lower *asymmetricus* Zones. *Po. l. mucronatus* is known from the Middle and Upper *varcus* Subzones in Germany (Ziegler *et al.* 1976, tables 1, 10-15). Representatives of the *Po. varcus* group and *Po. l. linguiformis* are abundant at Mount Wise and provide valuable information on intraspecific variability. The lanceolate polygnathids in this Fauna may be referred to three form species: *Po. ansatus*, *Po. timorensis* and *Po. varcus*. Of these, *Po. ansatus* is the most abundant and displays considerable variation, while *Po. varcus* is rare and *Po. timorensis* is identified principally on the basis of large growth stages like that of the holotype. These three species have frequently been recorded in association (Ziegler *et al.* 1976, tables 6, 7, 10-15), which by definition (*op. cit.*, p. 113) corresponds to the Middle *varcus* Subzone. Additional elements in the Mount Wise fauna are *S. brevis* and *S. planus*. The latter, which is found in several other *varcus* Zone faunas in Plymouth, has been recorded first from the Lower *obliquimarginatus* Zone (Ziegler 1971), but I suspect that the form identified in Fauna 9 represents the O<sub>1</sub> element in a polygnathid apparatus (*Po. varcus* s.l.).

Those elements of Fauna 9 other than *Po. tuberculatus* are consistent with a Middle

*varcus* Subzone age. The absence of species characteristic of the Upper Subzone and of younger zones suggests that *Po. tuberculatus* should be regarded as appearing within the Middle *varcus* Subzone. However it is worth noting here that the complete absence of *Icriodus* at Mount Wise is very likely the effect of some ecological control (see also Ziegler *et al.* 1976, p. 115); might other taxa be similarly excluded?

Indirect evidence for the age of Fauna 10 comes from the associated shelly fauna at Mount Wise (see Davidson 1864–5, p. 124; Ussher 1907, p. 53). Although this fauna has not been the subject of recent study, it clearly has a great deal in common with that of the Lummaton Shell Bed (within the Tor Bay Reef-Complex) which has also yielded the goniatite *Maenioceras terebratum*. The Lummaton Shell Bed is regarded as highest Middle Devonian in age (House *et al.* 1977; see also Matthews 1970) or, by implication, no younger than the uppermost Middle *varcus* Subzone in age (see House and Ziegler 1977).

*Fauna 10* (H1, West Hoe): A sparse and poorly preserved conodont fauna from the massive limestones on the northern margin of West Hoe Park (text-fig. 5e/1; SX47445387) includes a distinctive fragment of *Po. cristatus*, a species which appears in the upper part of the *hermanni-cristatus* Zone and ranges into the Middle *asymmetricus* Zone (Ziegler 1971, chart 3). Other polygnathids present are referred to *Po. cf. asymmetricus* and *Pa. cf. disparilis*, which support an *asymmetricus* Zone age. In the absence of *Ancyrodella* this Fauna is equated with the Lowermost *asymmetricus* Zone.

*Fauna 11* (WK00–04, Western King; EK61, Eastern King Point; R117, 8–9, Radford Quarry): On the coast at Western King (text-fig. 4c/WK01–04, 1–2; SX46065331), pale red crinoidal limestones include the following conodonts: *A. rotundiloba alata*, *A. aff. rugosa*, *Po. asymmetricus ovalis*, *Po. dengleri*, *Po. dubius* and *I. aff. subterminus*. This association is indicative of the Lower *asymmetricus* Zone (Ziegler 1971). At Eastern King Point (text-fig. 4c/61; SX46665347), similar limestones have yielded *A. rotundiloba* and a few very small palmatolepids.

On the east side of Plymouth, limestones in the south of Radford Quarry (text-fig. 4g/117, 9, 8; SX50525300) have also yielded *Po. asymmetricus* and *A. rotundiloba*, in this case in a fauna dominated by *I. symmetricus*. This fauna is regarded as the approximate time-equivalent of the faunas from Western King.

*Fauna 12* (DS1, Durnford Street; C135, Barn Pool; ?HL11, Hooelake Quarry): At the northern end of the Durnford Street roadcut (text-fig. 4c/DS1; SX46395369), fine-grained grey limestones have yielded a rich, but poorly preserved association. The conodonts (which are white in colour) include *Po. asymmetricus* subsp., *A. aff. gigas*, *Pa. aff. disparilis*, *Pa. aff. subrecta* and *Pa. sp(p)*. indet. The author has seen *Po. asymmetricus* n. subsp. A in collections from the Middle *asymmetricus* Zone of Nismes, Martouzain-Neuville and Hon in Belgium (collections of Drs. Mouravieff, Coen, and Coen-Aubert, Louvain-la-Neuve). Elsewhere, the form is recognized in faunas of a similar age in Austria (Flajs 1966) and North America (Pollock 1968). *A. aff. gigas* also suggests a Middle *asymmetricus* Zone age. No particular significance can at present be attached to the occurrence of the *Palmatolepis* species.



*A. gigas* has been found in sparse faunas from Barn Pool (text-fig. 4e/135; SX45645317) and questionably in Hooelake Quarry (text-fig. 4f/11; SX49575306) where fragmented palmatolepids are associated. Distinctive nothognathelliform elements are characteristic of some faunas from Barn Pool. These faunas are also tentatively linked to the Middle *asymmetricus* Zone.

The limestones lying above the Fauna 11 in Radford Quarry (text-fig. 4g/7-3; SX50585310) have yielded for the most part only poorly preserved polygnathids which cannot be referred to a particular zone. The same is true in Western King, where comparable limestones may be repeated by strong faulting which is evident along that coast.

*Fauna 13* (WK07-8, 56H): Due south of the most north-westerly bunker on Western King (text-fig. 4c; SX46085329), a faulted segment of pale red crinoidal limestone (c. 5 m thick) has yielded *Po. asymmetricus*, *A. rotundiloba* and *A. nodosa*. This association is not predicted by the known ranges of these species since the first two are not known to range outside the *asymmetricus* Zone (Ziegler 1971) whereas *A. nodosa* is regarded as no older than the *Ancyrognathus triangularis* Zone. Fauna 13 is provisionally linked to the base of the latter Zone and the top of the preceding *asymmetricus* Zone; the possibility exists that the faunas are admixed. *A. nodosa* has also been found in a limestone, on the east side of Western King (text-fig. 4c/56H; SX46225334), associated with infills (see below).

*Fauna 14* (R1, Radford Quarry; DS14, Durnford Street; FQ77, Fisons Quarry): This association includes *A. curvata*, *Pa. subrecta* and *Ancyrognathus triangularis*, which together indicate the *An. triangularis* Zone (although all are known from younger zones). The Fauna is best developed in Fisons Quarry, Cattedown (text-fig. 5a/77; SX49315377) where the red matrix of the conglomerate and associated red calcareous sediments on the north wall have also yielded *I. symmetricus* and *Po. webbi*.

Elsewhere, similar but much sparser faunas are identified within a fine-grained, pale red limestone at the southern end of Durnford Street (text-fig. 4c/DS14; SX46385362; this lies 56.3 m above Fauna 12) and at the northern end of Radford Quarry (text-fig. 4g/1; SX50485315). In both these faunas, fragmented indeterminate palmatolepids are also found.

*Fauna 15* (WK6, 13b, 56, b1, b2, Western King): The youngest conodont faunas from within the Plymouth Limestone comes from Western King (e.g. text-fig. 4c/13b; SX46145326). There, red calcareous shales and associated sediments have yielded an abundant early Famennian conodont fauna including several possibly reworked elements. The most common forms are *Pa. triangularis*, *Pa. delicatula* subsp., *Pa. subperlobata* and *I. alternatus*; less common are *Pa. minuta*, *Pa. perlobata*, *Pa. tenuipunctata* and a few specimens which are very close to *Pa. quadrantinosalobata*. This association is indicative of the Upper *Pa. triangularis* Zone, but the presence of *A. curvata* and *Ancyrognathus cryptus*, which are not known above the Middle part of that Zone, as well as indeterminate palmatolepids of possibly older horizons, suggests that some stratigraphic admixture has occurred (see Orchard 1975). Infills



within some limestones in Western King have yielded *Pa. tenuipunctata* and *Pa. delicatula* (see below).

A single specimen of *Pa. termini* from the northernmost limestones of Radford Quarry (text-fig. 4g/119; SX50405314) indicates an even later Famennian age: the species is found within the Middle and Upper *crepida* Zone in Germany. Once again, this form occurs within a fragmented palmatolepid fauna, thus lending support to the suggestion that these youngest limestones contain reworked, residual faunas.

#### THE STRATIGRAPHICAL HISTORY OF THE PLYMOUTH AREA

The following account is based largely on the preceding account of the conodont faunas and the conclusions regarding their ages. In some cases, the coral-based correlations of Taylor (1951) of sections devoid of conodonts has been followed; reference to these are given in the Appendix. Figures in parentheses are as in the previous section.

*Early Eifelian* (Faunas 1, 2): During the early Eifelian, the dark argillites (seen in Jennycliff Bay, SX490522) which had been accumulating in the Plymouth area, became intercalated with calcareous lithologies. Thin crinoidal limestones appear and become more frequent toward Dunstone Point (SX489526) where several metres of dark argillaceous platy limestones are developed. These bear a pyritized microfauna of bryozoans, ostracodes, gastropods and dacryoconarids (*Nowakia*) in addition to conodonts, principally icriodids. A similar fauna is forthcoming from several of the limestone horizons to the south of Dunstone Point and also from a small outcrop in similar limestones brought up by a fault at the southern end of Richmond Walk (SX459541). The latter, although they are thought to be a little younger, indicate that this particular facies was widespread. In terms of European models, the faunal association is Hercynian (Bohemian) (see Erben 1962, 1964); it includes elements of both the *Zone profunde* and *Zone quiescente* of the basinal bathymetric scheme of Lecompte (1968, pl. 4, p. 26).

The rich fossil horizon in shales outcropping in the Laira Bridge cutting (SX500543) includes small horn corals, atrypid brachiopods, fenestellid bryozoans, ostracodes and *Pleurodictyum* associated with large-eyed trilobites: the *Ruben-Riffe* biotype of German authors (Struve 1963). Dr. C. Burton (written comm., 1971) has identified within the trilobite fauna elements of both Rhenish (phacopids) and Bohemian (otariionid) aspect. This association, which has not been found elsewhere in Plymouth, is probably older than Eifelian, and indicates the existence of a 'mixed facies' prior to the onset of widespread carbonate deposition.

*Mid Eifelian* (Faunas 3-4): The deposition of platy crinoidal limestones evident during the low Eifelian is thought to have persisted into the mid Eifelian. Limestones in Faraday Road (FR1-7; SX498542) do not bear the distinctive microfauna but are otherwise similar to those developed during the early Eifelian. It is not possible to establish total thicknesses, but at least 35 m of these limestones and interbedded shales are seen in Faraday Road. Since Faunas 1 and 2 are regarded as representing levels below those seen in this area, it is probable that a substantial thickness of flaggy crinoidal limestones form an underlying basement for subsequent reef growth.

There also appears to have been a good deal of volcanic activity at this time. Tuffs (total c. 17.5 m) of variable composition are seen overlying the crinoidal limestones in Faraday Road and tuffs are seen also in close proximity to Fauna 2 in Richmond Walk. North of Dunstone Point (see text-fig. 3), volcanics have been traced by Ussher (1912) bordering the Limestone outcrop (but in uncertain relationship with it) to the east at Hooelake, Plymstock and beyond (text-figs. 1-3). To the west, thick green tuffs can be seen on Drake's Island (SX467529), along the Empacombe coast (in Cornwall) and in Southdown Quarry (SX435528). Tuffs are seen again in the extreme north of Richmond Walk (SX46095442) and are also recorded in the logs of ditches and boreholes within the City of Plymouth (see Ussher 1907, pp. 59-61).

In the midst of the volcanics in Faraday Road, the stromatoporoid bearing limestone (which has yielded Fauna 4) is thought to represent the first such development within the Plymouth Limestone. To what extent this development was facilitated by the preceding volcanism is uncertain although several authors have suggested that such activity aided in the formation of shallow shoals on which some Devonian carbonates accumulated. The stromatoporoid limestone development in the Princeroock area (it has not been found elsewhere) was relatively shortlived however and volcanism may equally have been responsible for the destruction of the organisms (see also Richter 1965, Holwill 1966). Limestone rafts and clasts within the volcanics on Drake's Island (text-fig. 4d/4, 5; SX467529) bear witness to the destructive events to which these early carbonates were subjected.

*Late Eifelian* (Fauna 5): The late Eifelian in Princeroock is represented by dark, thin-bedded and argillaceous, crinoidal limestones. Within the lower horizons there is a lot of interbedded shale, but the beds become increasingly calcareous upward (to the south). These limestones contain pyritized hexactinellid sponge spicules and the phosphatic remains of fish, but corals are uncommon. Both in Princeroock and in the coeval limestones in Teats Hill Quarry, Coxside (text-fig. 5c/44; SX486541), the conodont faunas are dominated by the simple cone group (principally *Belodella*) which generally comprises 50-80% of the faunas (in terms of individual elements); icriodids and polygnathids occur in approximately equal numbers.

Slightly younger argillaceous beds than those yielding Fauna 5 conodonts in Teats Hill Quarry (text-fig. 5c/46), contain numerous rugosans, particularly cystifers, and large limestone clasts of massive colonial rugose and tabulate corals, and stromatoporoids. Similar bioclastic beds have also been identified in Princeroock (SX49735417). Immediately above these beds (which are c. 3 m thick) in Teats Hill Quarry, there are 'thickets' of small-stemmed fasciculate corals. These beds are thought to have accumulated in relatively quiet waters, which occasionally received the eroded products of vigorous wave or current action nearby.

West of Coxside, there is no visible evidence of widespread carbonate deposition during the late Eifelian. In the eastern outcrop, there are probable equivalents in Saltram Quarry (text-fig. 3; SX509543) and in Hooelake Quarry (text-fig. 4f; SX496528) where Taylor (1951) has established equivalence with the Princeroock sequence on the basis of the coral faunas. However, for the most part the limestones south and west of the Cattewater are relatively barren, *Amphipora* being the most conspicuous element of the rare fossil horizons.

*Early-mid Givetian* (Fauna 6): In the south-east, in Hoelake Quarry, argillaceous *Amphipora* micrites with occasional solitary rugosans, tabulates and stromatoporoids (some with invaginated flanks) characterize inferred low-mid Givetian strata. The probable equivalents in Pomphlett Quarry (SX505543) and in Saltram Quarry (SX509543) include muddy intraclasts which Braithewaite (1966, p. 187; 1967, p. 298) has cited as evidence of erosion of consolidated carbonate mud synchronous with normal limestone deposition.

In Princeroak, the section continues through Cattedown Quarry (SX494539) and the Gasworks Quarry (SX492539) where the lower horizons are predominantly pelsparites and calcilitites (Braithewaite 1966, p. 185). Associated beds of comminuted shelly debris yield rich conodont faunas. Southward through Cattedown the limestones become thicker bedded, less argillaceous and increasingly fossiliferous. Prolific coral-stromatoporoid faunas in which an encrusting mode is increasingly common can be seen on the west wall of the Gasworks Quarry; these limestones do not yield conodonts. Tsien (1974, p. 23) regards the encrusting morphology as an adaptation to increased salinity and decreased water circulation. However, interbedded bioclastic material in much of the Cattedown section must reflect the periodic influence of strong currents. In places (SX49435377, SX49255370), large massive stromatoporoids are common.

The conodont faunas from northern Cattedown continue to be dominated by *Belodella*, but the linguiform group of polygnathids and robust icriodids of the *expansus* group are well represented. The questionably coeval faunas in Coxside (SX486540) and on Drake's Island (SX469529) are characterized by a paucity of species which may indicate either effective current sorting or some ecological control.

Beyond the Limestone's edge to the north-west, equivalent strata at Neal Point (SX436613) consists of limestone turbidites interbedded with styliolinid shales. Conodont faunas from these limestones are similar in composition to those from Cattedown.

*Late Givetian* (Faunas 7-9): In Hoelake (SX495530) and Pomphlett Mill (SX508538) Quarries, the carbonates continue to be comparatively barren. In contrast, the southern limestones of Cattedown (e.g. Fisons Quarry, text-fig. 5a; SX494537) are richly fossiliferous biomicrites. Massive stromatoporoids and tabulate corals are common, while *Amphipora* fills some beds in the southernmost outcrop (SX49515356).

In the west around Stonehouse (text-fig. 3), the oldest limestones are seen at the northern end of Richmond Walk (SX461544). There, thin, irregularly-bedded bituminous carbonates bear a rich fauna of heliolitid tabulates, lamellar stromatoporoids, and solitary rugosans. The conodont faunas are dominated by *Belodella* and polygnathids, but *Icriodus* is absent from these, and from virtually all known Givetian limestones throughout this western area. Perhaps significantly, the only icriodids found are those from within the *latericrescens* interval (see above), which corresponds approximately with the basal beds of the thicker-bedded to massive pale limestones which characterize the main outcrop of Richmond Walk. These latter carbonates include bioclastic packstones and wackestones (see Braithewaite 1967, pp. 295, 297) while some horizons seen on the long east wall (SX46005438) contain



massive stromatoporoids, although these are not as widespread as in the probable correlatives in Cattedown, nor do they appear to be *in situ*.

Shell beds were developed in the proximity of the Limestone's edge at Mutton Cove (SX453540) and Mount Wise (SX456540) during the latest Givetian. They are thought to represent local, lenticular concentrations similar to those at Lummaton (see Elliot 1961) and Wolborough in the Torbay area. Shell beds were also known from 'the Dockyard' and 'St. Georges Hall' in Stonehouse but the localities no longer exist for study. In the Mount Wise fauna (Fauna 9), the simple cones, the lanceolate and linguiform polygnathids are about equally represented; *Icriodus* is totally absent in the fauna of well over a thousand elements.

Beyond the Tamar, a lane section near Botus Fleming (SX410612) is developed in *Styliolina* shales, in part calcareous, and includes lenses of coarse crinoidal limestone which have yielded pyritized stick bryozoans, smooth ostracodes, *Nowakia*, gastropods and also a single indeterminate goniatite protoconch, an association very similar to that which characterizes the lowest horizons of the Plymouth Limestone (Faunas 1, 2).

*Early-mid Frasnian* (Faunas 10–13): Conodonts from near the top of the massive stromatoporoid limestones of West Hoe (text-fig. 5e/H1; SX474539) confirm that this particular facies persisted into the Upper Devonian, as is thought to be the case in southern Cattedown where similar limestones are undated. The limestones exposed at Devils Point (SX460533) and on the western foreshore of Western King are thought to be equivalent: these bear a diverse coral fauna but no conodonts have been found. Toward Western King Point (SX461533), and also at Eastern King Point (SX466535), the Lower *asymmetricus* Zone (Fauna 11) is represented by distinctive thin beds of pale red crinoidal limestone with red shale interbeds and partings. Slightly higher beds are thicker but include a similar macrofauna of extensive, probably *in situ* lamellar stromatoporoids and *Alveolites*. The Western King section was thought by Taylor (1951) to be inverted, but younger conodont faunas appear, albeit sporadically, toward the south, downdip. However, there is probably repetition along this coast as a result of the frequent faulting. About 17 m downdip from limestones yielding Fauna 11, but separated from them by at least one fault, there are the lithologically similar, richly fossiliferous limestones bearing Fauna 13; some horizons there are crowded with rugosans, the white colour of which contrasts strikingly with the red lime matrix (noted by Hennah 1822, pp. 12–13). The thin red beds bearing Faunas 11 and 13 are interpreted as representing intervals of deepening. The conodont faunas from these limestones are diverse and relatively rich with *Ancyrodella* and the wide plated polygnathids figuring prominently, although *Palmatolepis* is very rare. The thick-bedded to massive grey limestones intervening between Faunas 11 and 13 in Western King, and thought to be equivalent to those which have yielded Fauna 12 in Barn Pool (SX456532) and Durnford Street (SX464537), are regarded as representing a return to shallower water conditions, less favourable to conodont-animals (or the preservation of their remains).

In the east, limestones bearing Fauna 11 in Radford Quarry (SX505532) are also thin-bedded limestones with a large red argillaceous component, although they differ from the coeval beds in Western King in being darker and lacking macrofossils.



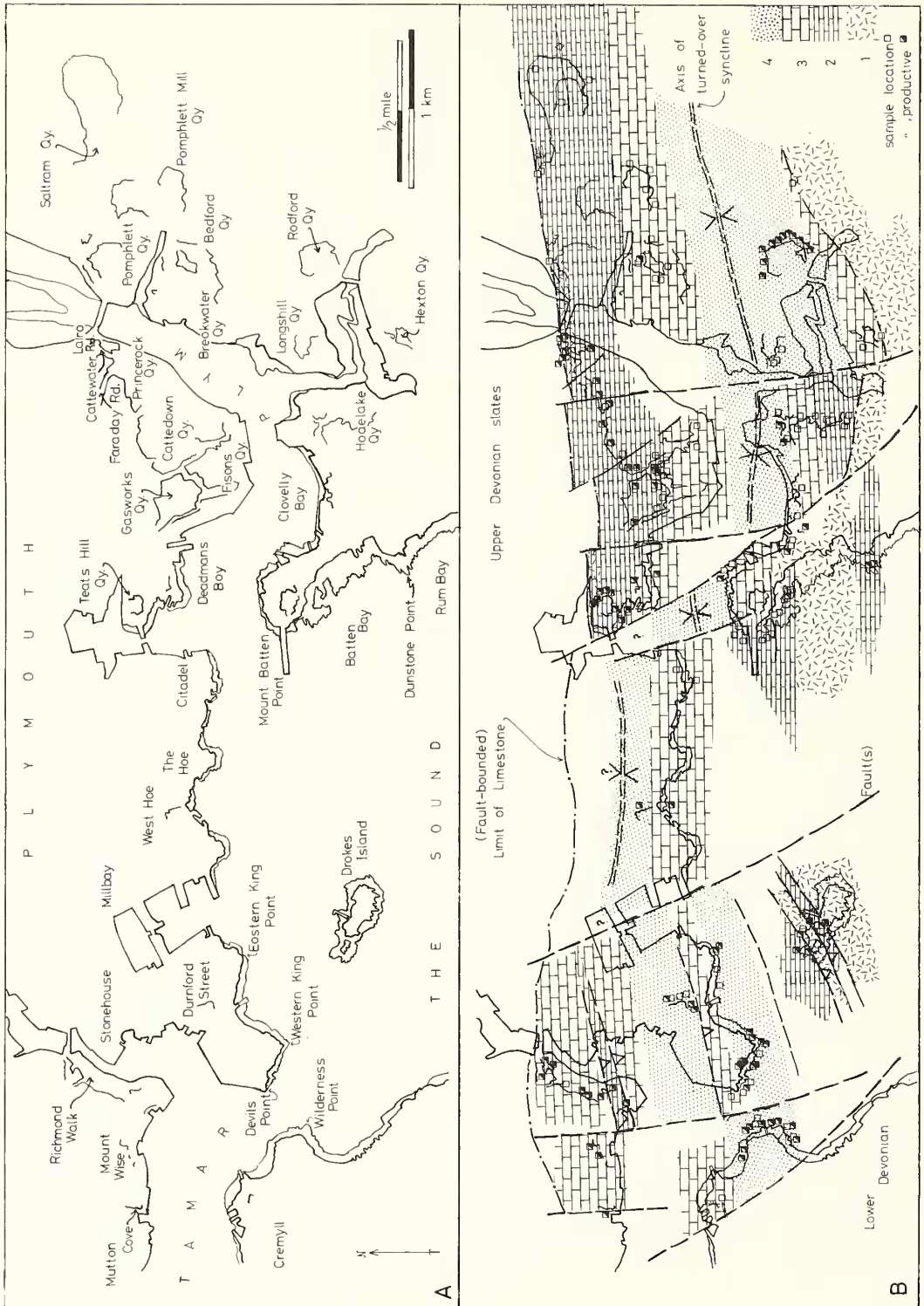
There, the conodont faunas are dominated by *Icriodus*, with the lanceolate polygnathids of secondary importance; both *Ancyrodella* and *Po. asymmetricus* are rare. The younger limestones in Radford Quarry (updip, the section is inverted) are, like those of Western King, thicker, less argillaceous and yield only a few poorly preserved polygnathids. Unlike the carbonates in the west, the Radford limestones remain barren, and there is no sign of renewed deepening as in Western King.

*Mid Frasnian-early Famennian* (Faunas 14, 15): The Fisons Quarry conglomerate (SX493538), first described by Braithewaite (1967, p. 313), is composed of grey, well-rounded clasts set in a red lime-mud matrix. The latter is dated as *A. triangularis* Zone in age whereas the containing limestones are regarded as mid-late Givetian; the clasts are undated although they are apparently unfossiliferous, unlike the host limestones. It is suggested that the conglomerate represents the infill of a crevasse within the older limestones.

Contemporaneous with the suggested fissuring of the limestones in Cattedown, normal carbonate deposition appears to have continued in Radford Quarry (SX505532) and in Durnford Street (SX464536), although this may have been very slow. Fragmented, questionably admixed conodont faunas from the northernmost outcrop in Radford Quarry (SX504531) may represent an interval during which there was a prolonged period of standstill or active erosion and weathering (solution).

Green-grey unfossiliferous argillites are seen directly overlying limestones in Langshill Quarry (text-fig. 3; SX49945316), but neither are dated (this section is thought to be inverted, as in the neighbouring Radford Quarry). Red calcareous shales are seen on the northern margin of Hoelake Quarry (e.g. SX49615311) and in the Breakwater Quarry (SX50405386), but these beds have not yielded conodonts. On the contrary, in Western King (SX46145326) red, occasionally crinoidal, calcareous shales have yielded abundant, variably preserved conodonts (Fauna 15), as well as a lot of fish teeth and scales. A large part of this shale in Western King is found adjacent to, and caught up in, the numerous faults which dissect the grey Frasnian limestones. In places, large rafts of grey limestone are seen in the shale, and limestone breccias are also developed. It is assumed that the red calcareous shales originally overlay the limestones. The extent to which the limestones within the shale are the result of post-depositional tectonic 'squeezing' is uncertain; some may be the product of sedimentary rafting (megabrecciation) during collapse of the reef. However, the time interval between Faunas 14 and 15 is largely unaccounted for. It is possible that some of the undated coral-stromatoporoid limestones in Western King represent some or all of this interval, but I am inclined to regard these as repeated outcrop of the older Frasnian limestones. A further possibility arises from the presence of the anomalous elements in Fauna 15 (see below).

Within a number of the Frasnian limestone segments in Western King, red, pink, and grey laminated micrites occur irregularly within the grey host limestones. These have been interpreted as the infillings of solution cavities (see Braithewaite 1967, Orchard 1975). The infilling material has yielded a few conodonts indicative of the early Famennian and the author has previously discussed the genesis of the sediments (*op. cit.*). They are thought to have developed as a consequence of the dissolution of the Frasnian limestone prior to the subsidence represented by the associated



TEXT-FIG. 3A. Plymouth localities, see Figs. 4, 5 for details. 3B. Age and structure of the Plymouth Limestone; minor faults omitted. Key: 1. Volcanics and argillites, Eifelian. 2. Limestones, Eifelian, pre-*varcus* Zone. 3. Limestones, *varcus* Zone to pre-*asymmetricus* Zone. 4. Limestones and calcareous shales, *asymmetricus* Zone and younger.

sediments bearing Fauna 15. The older conodonts present in Fauna 15 might be regarded as the residue of this dissolution.

Evidence from the Torpoint area (west of the Tamar) and from areas to the north of the Plymouth Limestone indicate the establishment of the basinal ostracod-slate facies during the Frasnian (Gooday 1975; see text-fig. 1).

#### SUMMARY AND CONCLUSIONS

The stratigraphical history of the Plymouth Limestone begins early in the Eifelian. By then (Faunas 1, 2), sediments of Rhenish or mixed magnafacies had given way to those of Hercynian aspect (*sensu* Erben 1962), as Plymouth became the site of widespread carbonate deposition. The accumulation of flaggy crinoidal limestones persisted into the mid Eifelian (Fauna 3) and represent a substantial carbonate foundation for subsequent reef growth. This was added to during the mid Eifelian when there was an interval of widespread volcanic activity, which probably resulted in a generally shallower environment. Locally, the development of stromatoporoid limestone was initiated (Fauna 4), but these were swamped by the products of further volcanism.

Later in the Eifelian and during the early Givetian (Faunas 5, 6), renewed carbonate deposition became widespread in the eastern areas but is unknown west of Coxside. Upward the limestones become increasingly fossiliferous and are comparable to the *Schwelm* facies of Krebs (1968, pp. 297-298: an association of stromatoporoids and corals which do not constitute a wave resistant structure). By the late Givetian (Faunas 7-9), a shallow-water carbonate complex was well established in the Plymouth area. At this time, limestone deposition appears to have reached a maximum spread, appearing in the west around Stonehouse, perhaps for the first time. The massive stromatoporoids are a relatively small part of the prolific 'coralline' growth which flourished in the area of Cattedown, but together these 'biogenic structures' resulted in a degree of facies differentiation (as in the *Dorp* facies of Krebs 1968). Thus areas in the east (Saltram-Pomphlett) and southeast (Hooe) display the characteristics of a partially restricted environment and are interpreted as having lain 'back-reef'; no conodonts have been found in the Middle Devonian limestones of these areas. In the western outcrop, the oldest bedded limestones date from the *varcus* Zone and include coarse bioclastics (Richmond Walk) and shell beds (Mount Wise); the abundant conodont faunas from there do not include icriodids. These western limestones are interpreted as having developed on the seaward side of the complex, which may have spread (north-?) westward during the Givetian. North of the Limestone, and west of the Tamar, the Middle Devonian is developed in pelagic argillites with limestone turbidites.

The massive limestones of The Hoe and probably those of southern Cattedown extend into the Upper Devonian. Within the Lower *asymmetricus* Zone, limestones on both the western and eastern flanks of the Limestone are interpreted as representing an interval of deepening. In the west (Western King, Barn Pool, Durnford Street), the Middle *asymmetricus* Zone is developed in massive limestones but during the Upper *asymmetricus* Zone (Fauna 13) there was, in Western King, a return to the deeper-water conditions which prevailed during the Lower *asymmetricus* Zone. The



comparable horizons in Radford Quarry continue to be developed in massive limestone. In Cattedown however, during the *A. triangularis* Zone (Fauna 14), deep crevassing of the massive Givetian limestones is thought to have occurred. Stratigraphical admixture of the faunas from the youngest limestones in Radford and Hooelake Quarries (and in Fauna 15), the close stratigraphical proximity of these to older faunas, and the evidence of carbonate dissolution in Western King, suggests that there was a period of time during which active sedimentation ceased and an unknown thickness of Plymouth Limestone may have been removed. This has given rise to the suggestion (Orchard 1975) that the Plymouth Limestone persisted as a topographic high within the late Devonian sea whilst pelagic ostracode-slates were being deposited in areas to the north and west.

These pelagic areas adjacent to the Plymouth Limestone lay in what has recently been termed the Trevone Basin by Matthews (1977, p. 108), who suggested that the massive Devonian carbonates in South Devon developed on the southern margins of this Basin. The facies disposition within the Plymouth Limestone, as interpreted, would seem to support this hypothesis, although there remains a question mark over the relationships to the east and south; there must have been an effective barrier to circulation in that direction. Be that as it may, the idea of a 'locally unstable . . . structurally active' Trevone Basin adjacent to a Plymouth *Schwelle* is useful also in explaining the Frasnian and early Famennian events in Plymouth such as the intervals of deepening and uplift which were likely associated with the suggested crevassing and reworking.

In Germany, 'dead reefs' such as that which I suggest persisted on the site of Plymouth, are known to have remained exposed until mid Lower Carboniferous times before they were totally overtaken by sediment (e.g. see Krebs 1968, p. 304); similar reefs have been described from Canada (Pollock and Fuller 1972). The possibility that the Plymouth Limestone, or areas within it, remained above the level of sedimentation for some considerable time cannot be ruled out. In this connection, it is noteworthy that reworked Upper Devonian conodonts have been found in Lower Carboniferous sediments in East Cornwall (Matthews 1969, pp. 265-266), although these are indicative of younger stratigraphical levels than are seen in Plymouth, at present.

#### SYSTEMATIC PALAEOLOGY

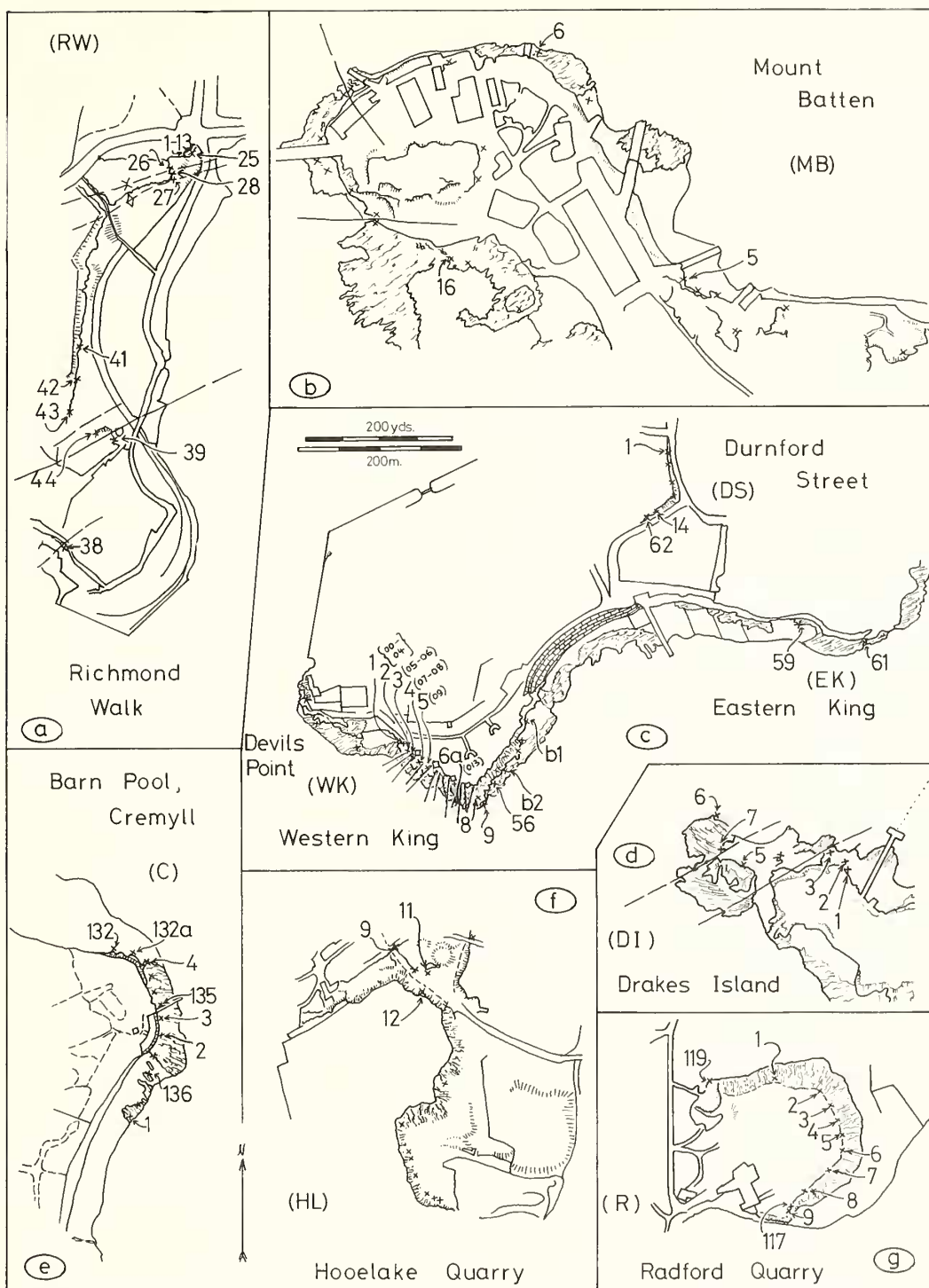
The following is a form-taxonomy; only platform elements are considered here. The figured material is housed in the Sedgwick Museum, Cambridge (all bear the prefix SM). Additional material is deposited in the Department of Geology, University of Hull.

*Ancyrodella curvata* (Branson and Mehl). Plate 114, figs. 2, 8-10, 20 = 1934 *Ancyrognathus curvata* n. sp.—Branson and Mehl, p. 241, pl. 19, figs. 6, 11.

*Ancyrodella gigas* Youngquist. Plate 114, fig. 4 = 1947 *Ancyrodella gigas* n. sp.—Youngquist, pp. 96-97, pl. 25, fig. 23.

*Ancyrodella* aff. *gigas* Youngquist. Plate 114, figs. 1, 11, 12.

*Remarks:* Specimens included here bear a shorter, relatively broader platform than *A. gigas*. A similar specimen has been figured by Miller and Youngquist (1947, pl. 74, fig. 13) and such forms are known to



TEXT-FIG. 4a-g. Plymouth localities: detail of exposure and sample location (productive samples only).



occur also in the Belgian Frasnian (pers. comm., Mouravieff 1974). Specimens referred to *A. gigas* by Szulcowski (1971) and Uyeno (1974) on the basis of their aboral configuration also differ in platform outline from the holotype.

*Ancyrodella nodosa* Ulrich and Bassler. Plate 114, fig. 3 = 1926 *Ancyrodella nodosa* n. sp.—Ulrich and Bassler, p. 48, pl. 1, figs. 10–13.

*Ancyrodella rotundiloba* (Bryant). Plate 114, figs. 14, 15 = 1921 *Polygnathus rotundilobus* n. sp.—Bryant, pp. 26–27, pl. 12, figs. 1–6.

*Remarks*: A single specimen from Radford Quarry has a much longer platform development than is typical of *A. rotundiloba* subsp. and yet the secondary keel development corresponds to that of the latter, to which the specimen is tentatively referred.

*Ancyrodella rotundiloba alata* Glenister and Klapper. Plate 114, figs. 13, 16–19, 23, 25, 26, 29, 30, 32 = 1966 *Ancyrodella rotundiloba alata* n. subsp.—Glenister and Klapper, pp. 799–800, pl. 85, figs. 1–8, pl. 86, figs. 1–4.

*Remarks*: The alate forms of *A. rotundiloba* from Plymouth exhibit a variable keel development.

*Ancyrodella* aff. *rugosa* Branson and Mehl. Plate 114, figs. 6, 7 = aff. 1934 *Ancyrodella rugosa* n. sp.—Branson and Mehl, p. 239, pl. 19, figs. 15, 17.

*Remarks*: A few specimens from Plymouth are intermediate between *A. rotundiloba* and *A. gigas* in terms of their secondary keel development; such a position is occupied by *A. rugosa* (Ziegler 1962, fig. 2). However, the Plymouth specimens are relatively shorter than is typical of *A. rugosa*; they bear a conspicuously coarser ornament than associated specimens of *A. r. alata*.

*Ancyrognathus triangularis* Youngquist. Plate 114, fig. 5 = 1945 *Ancyrognathus triangularis* n. sp.—Youngquist, pp. 356–357, pl. 54, fig. 7.

*Ancyrognathus cryptus* Ziegler. Plate 114, figs. 21–22 = 1962 *Ancyrognathus cryptus* n. sp.—Ziegler, pp. 49–50, pl. 9, figs. 2–6.

*Icriodus alternatus* Branson and Mehl. Plate 109, figs. 27, 28, 33, 36–38, 40–44 = 1934 *Icriodus alternatus* n. sp.—Branson and Mehl, pp. 225–226, pl. 13, figs. 4–6.

*Icriodus corniger* Wittekindt. Plate 107, figs. 6, 10, 11; ?3, 8, 29 = 1966 *Icriodus corniger* n. sp.—Wittekindt, p. 629, pl. 1, figs. 9–12.

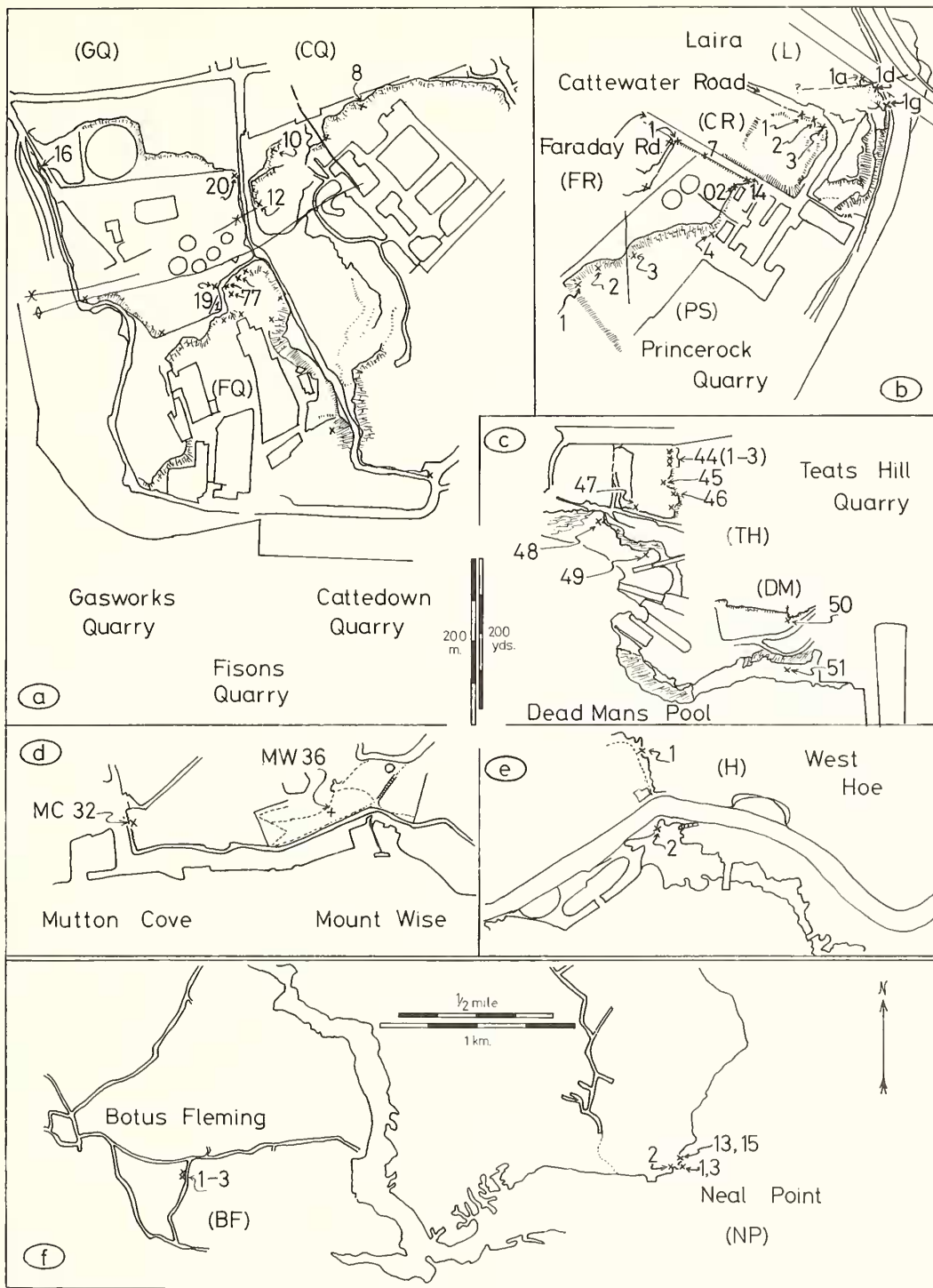
*Remarks*: *I. corniger* from Plymouth resembles the third morphotype of Bultynck (1972, pp. 76–78) but since the aboral margins of associated icriodids are generally broken, identification of *I. introlevatus* and *I. curvirostratus* is not possible. In some specimens included here, the anteriormost blade denticle is larger and lies higher than the other denticles; also transverse elongation of the lateral denticles is pronounced in large specimens. In these respects the forms approach *I. retrodepressus*, with which Bultynck (1972, p. 84, fig. 17) has linked *I. corniger* phylogenetically.

*Icriodus difficilis* Ziegler and Klapper. Plate 109, figs. 9, 12, 13, 16, 18 = 1976 *Icriodus difficilis* n. sp.—Ziegler and Klapper, in Ziegler *et al.*, pp. 117–118, figs. 1–7, 17.

*Icriodus expansus* Branson and Mehl group. Plate 109, figs. 2–5, 7, 10, 14, 15, 20, 23.

*Description*: Icriodids in which the platform is generally biconvex, and the axis usually straight. The median denticles tend to be round in oral aspect and those of the lateral rows oval and transversely elongate. Longitudinal ridges are only rarely developed and are never conspicuous whereas transverse ridges are common and often strong. The blade is relatively short and the posterior border is often inclined posteriorward. The aboral expansion is one third to one half the total unit length, is rounded on the outer side and may or may not include a spur on the inner side; the posterior edge is straight.

*Remarks*: Icriodids from both the Middle and Upper Devonian of Plymouth conform to a generalized concept described above and here called the *I. expansus* group. However, Middle Devonian representatives tend to be more strongly biconvex than those from the Upper Devonian while the latter tend to be relatively



TEXT-FIG. 5a-f. Further Plymouth localities: detail of exposure and sample location (productive samples only).

longer and narrower with more regular, closer spaced denticles. Both the anterior and posterior denticles of specimens from the Middle Devonian tend to be more prominent too. However, the material at hand is too sparse to permit a full evaluation of these observations.

During growth, the denticulation of these icriodids becomes increasingly robust and this is reflected in overall platform outline and in the profile of the blade. The larger specimens from Plymouth are similar to *I. arkonensis* Stauffer 1938 which has been regarded as a junior synonym of *I. expansus*, although Klapper (in Ziegler 1975) has considered the former distinct in bearing a prominent spur and sinus. The *I. expansus* group embraces specimens with spur development, but because of the poor preservation of the Plymouth icriodids the variability of the aboral outline is not known. It is, however, noteworthy that some icriodid taxa, for example *I. alternatus*, appear to include forms both with and without a spur (Schumacher 1971, p. 102).

*Icriodus latericrescens latericrescens* Branson and Mehl. Plate 109, figs. 6, 11 = p. 1938 *Icriodus latericrescens* n. sp.—Branson and Mehl, pp. 164–165, pl. 26, figs. 30–32, 34, 35.

*Icriodus obliquimarginatus* Bischoff and Ziegler. Plate 107, figs. 7, 9, 13, 14, 17, 18; Plate 109, figs. 1, 8 = 1957 *Icriodus obliquimarginatus* n. sp.—Bischoff and Ziegler, p. 62, pl. 6, fig. 14.

*Icriodus regularicrescens* Bultynck. Plate 107, figs. 15, 21, 23, 26–28, 31, 32 = v 1970 *Icriodus regularicrescens* n. sp.—Bultynck, pp. 111–112, pl. 7, figs. 1–7; pl. 8, figs. 2, 4, 7, 8.

*Remarks:* The Plymouth material includes specimens which show variation in the degree of alignment of the median and lateral rows, in the development of transverse bridges, and in the regularity of the denticulation. Furthermore, there appears to be some variation in the aboral outline; a few specimens (e.g. Plate 107, figs. 26, 27) appear to have a posterior-lateral projection similar to that of *I. corniger*.

*Icriodus retrodepressus* Bultynck. Plate 107, figs. 5, 33; ?1, 2, 4 = 1970 *Icriodus retrodepressus* n. sp.—Bultynck, pp. 110–111, pl. 30, figs. 1–6.

*Icriodus* aff. *subterminus* Youngquist. Plate 109, figs. 19, 21, 25, 30, 31 = aff. 1947 *Icriodus subterminus* n. sp.—Youngquist, p. 103, pl. 25, fig. 14.

*Description:* The axis is straight but may be incurved at the anterior end; platform margins are slightly biconvex to subparallel. The growth point is very short being composed of only a single denticle in continuation of the median denticle row. The middle platform consists of four or five discrete denticles in each row. The median denticles in the central part of the platform are large and round in cross-section, while those to the front and rear are smaller and laterally compressed. The lateral denticles are generally round

#### EXPLANATION OF PLATE 107

All figs.  $\times 35$ .

Figs. 1, 2, 4, 5, 33, ?3. *Icriodus retrodepressus* Bultynck. From Dunstone Point (MB23). 1, 2, 4. Inner lateral, aboral, oral views of H10079. 5. Oral view of H10081. 33. Oral view of H10082. 3. Oral view of H10080; juvenile.

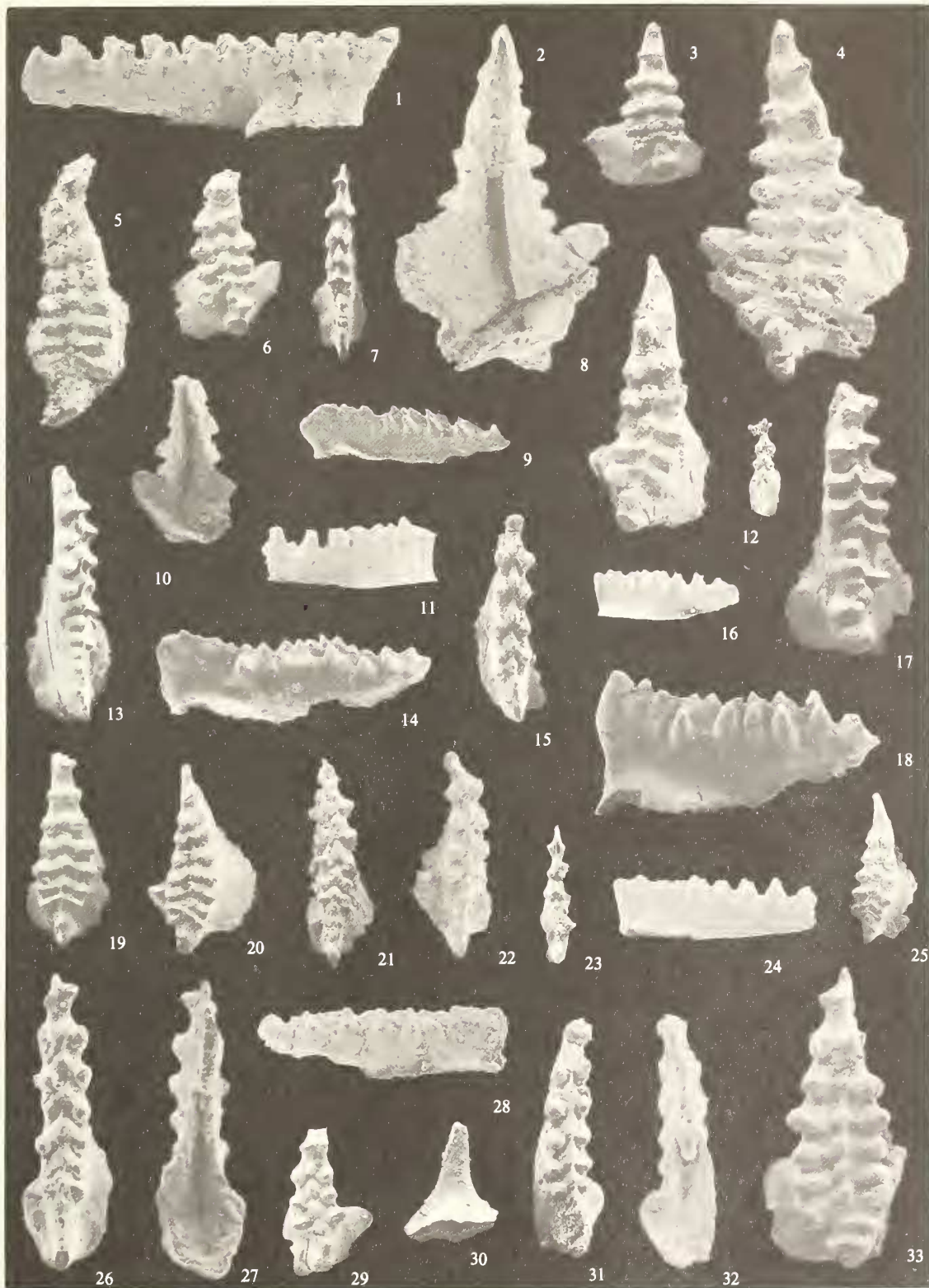
Figs. 6, 8, 10, 11, 29. *Icriodus corniger* Wittekindt. 6, 10, 11. Oral, aboral, lateral views of H10083. 8. Oral view of H10084. Both from Dunstone Point (MB23). 29. Oral view of H10085, Richmond Walk (RW39).

Figs. 7, 9, 13, 14, 17, 18. *Icriodus obliquimarginatus* Bischoff and Ziegler. From Princerock Quarry. 7, 9. Oral, lateral views of H10086, (PS3). 13, 14. Oral (oblique), lateral views of H10087 (PS4). 17, 18. Oral, lateral views of H10088, (PS4).

Figs. 16, 19, 20, 24, 25, ?12. *Icriodus* n. sp. A. From Richmond Walk (RW39). 16, 25. Outer lateral, oral views of H10090. 19, 24. Oral, lateral views of H10091. 12. Oral view of H10089; juvenile.

Figs. 15, 21, 22, 23, 26–28, 31, 32. *Icriodus regularicrescens* Bultynck. From Teats Hill Quarry (TH44/3), except Fig. 21—from Neal Point (NP2). 15. Oral view of H10092. 21. Oral view of H10093. 22. Oral view of H10094; note intercalated medians. 23. Oral view of H10095; juvenile. 26–28. Oral, aboral, lateral views of H10096. 31, 32. Oral, aboral views of H10097.

Fig. 30. Acodinan element. Durnford Point (MB23). Posterior view of H10098.



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in cross section and of equal size; the posteriormost one or two may be slightly elongate transversely and directed slightly anteriorward. In small specimens the denticles are alternate but these tend to become subalternate in later growth stages. Occasionally, the spacing of the denticles rows is irregular, the anterior denticles being further apart than the posterior ones. The blade is composed of three denticles, partially fused and increasing in size posteriorward; they are abruptly higher than the platform denticles in some specimens. Aborally, the gully expands progressively posteriorward to a point a little behind the unit midlength, beyond which the expansion of the bowl is probably symmetrical.

*Remarks*: The form resembles *I. subterminus* in the overall oral plan and the sometimes irregular denticulation, but does not bear the anterior denticles nor, in all cases, the high posterior denticles which characterize the latter. Specimens referred to *I. subterminus* by Klapper (*in* Ziegler 1975), do not exhibit high anterior denticles either, although some do display the irregular median denticulation.

*Icriodus symmetricus* Branson and Mehl. Plate 109, figs. 17, 22, 24, 26, 32, 34 = 1934 *Icriodus symmetricus* n. sp.—Branson and Mehl, p. 226, pl. 13, figs. 1–3.

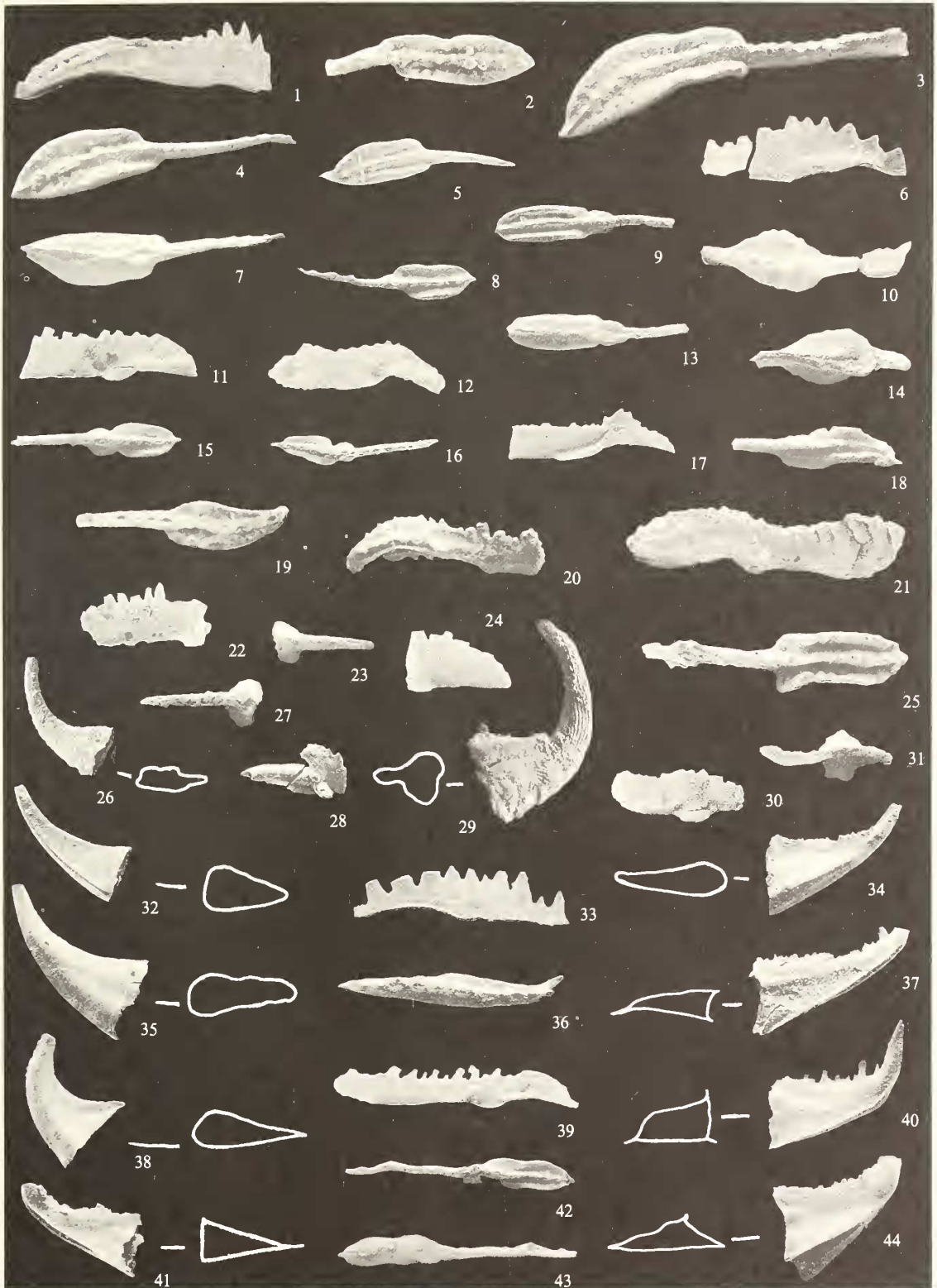
*Icriodus* n. sp. A. Plate 107, figs. 16, 19, 20, 24, 25, ?12.

*Description*: Platform biconvex, broadest near midpoint, and pointed at each end; the unit is straight or incurved anteriorward. The growth point is composed of two to three denticle series which are not well differentiated from the mid-platform. The latter bears three rows of four to six denticles. The medians are round in cross section and are largest about the middle of the platform, decreasing in size in both directions.

#### EXPLANATION OF PLATE 108

Figs.  $\times 35$ , unless qualified.

- Figs. 1, 3–5, 7, 8. *Polygnathus pseudofolius* Wittekindt. 1, 4, 7, 8 from Princerock Quarry (PS4). 1, 4, 7. Inner lateral, oral, aboral views of H10099. 3. Oblique-oral view of H10100, Teats Hill Quarry (TH44/3). 5. Oral view of H10101, Cattewater Road (CR3). 8. Oral view of H10102; juvenile.
- Figs. 2, 21, 25. *Polygnathus xylus ensensis* Ziegler and Klapper. 2. Oral view of H10103, Teats Hill Quarry (TH44/1); shows affinities with *Po. pseudofolius*. 21, 25. Lateral, oral views of H10104, Richmond Walk (RW28); posterior platform not flattened as in 2.
- Figs. 6, 10, 14. *Polygnathus angustipennatus* Bischoff and Ziegler *sensu lato*. Drake's Island (D16). Inner lateral, oral, aboral views of H10105.
- Figs. 9, 13. *Polygnathus xylus* Stauffer. Neal Point (NP15). Oral, aboral views of H10106; juvenile.
- Figs. 11, 12, 15–18. *Polygnathus timorensis*. Klapper, Philip and Jackson. Juvenile forms corresponding to '*Po. rhenanus*'. 11, 15. Lateral, oral views of H10107, Botus Fleming (BF3). 12, 16–18 from Richmond Walk (RW25). 12, 16. Inner lateral, oral views of H10108. 17, 18. Lateral, oral views of H10109; note high geniculation point.
- Figs. 19, 20, 33, 36. *Polygnathus aff. latifossatus* Wirth. Richmond Walk (RW25). 19, 20. Oral, inner lateral views of H10110. 33, 36. Lateral, oral views of H10120.
- Figs. 22–24, 27. *Spathognathodus brevis* (Bischoff and Ziegler). 22, 27. Lateral, oral views of H10111, Botus Fleming (BF3). 23, 24. Oral, lateral views of H10112, Richmond Walk (RW25).
- Figs. 26, 29. Panderodiform elements. 26. Obverse view of H10113, Deadman's Bay (DM51). 29. Obverse view of H10114, Teats Hill Quarry (TH44/2).
- Fig. 28. *Ozarkodina expansa* (Uyeno and Mason).  $O_1$  element of multielement *Pandorinellina* sp. Cattewater Road (CR3). Lateral view of H10115.
- Figs. 30, 31. *Spathognathodus bidentatus* Bischoff and Ziegler. Teats Hill Quarry (TH44/3). Lateral, oral views of H10116; deformed specimen.
- Figs. 32, 35, 38. *Coelocerosodontus* sp(p). Mount Wise (MW36). Lateral views of: 32. H10117; specimen with incipient costa. 35. H10118. 38. H10119; strongly recurved specimen.
- Figs. 34, 37, 40, 41, 44. *Belodella* sp(p). Mount Wise (MW36). Lateral views of: 34. H10121, '*B. devonicus*'. 37. H10122, 41. H10123, both '*B. resimus*'. 40. H10124, 44. H10125, both '*B. triangularis*'.
- Figs. 39, 42, 43. *Polygnathus timorensis* Klapper, Philip and Jackson. Neal Point (NP15). Lateral, oral, aboral views of H10126,  $\times 25$ .



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The laterals are generally transversely elongate and are largest at platform mid-length. In most specimens the two posteriormost lateral denticles are distinctly smaller than the others. The median denticles are slightly displaced anteriorward with respect to the laterals. Transverse ridges are well developed in the posterior platform, progressively less so anteriorward. The blade is composed of two or three partially fused denticles which are set higher than those of the middle platform. The posterior border is inclined. The basal outline, although not known in detail, is characterized by a broad expansion beginning well in front of the unit midlength on the outer side. In one specimen there is a suggestion of a spur.

*Remarks:* This species differs from members of the *I. expansus* group in the character of the blade and in the relatively small size of the posterior lateral denticles, although this latter character has also been observed in the *I. expansus* group (e.g. Plate 109, fig. 2). A specimen illustrated, in lateral view only, by Seddon (1970, pl. 4, fig. 22) has a very similar blade development.

*Palmatolepis delicatula delicatula* Branson and Mehl. Plate 115, figs. 6, 7, 12, 13 = 1934 *Palmatolepis delicatula* n. sp.—Branson and Mehl, p. 237, pl. 18, figs. 4, 10.

*Palmatolepis delicatula clarki* Ziegler. Plate 115, figs. 9, 11 = 1962 *Palmatolepis marginata clarki* n. subsp.—Ziegler, pp. 62–65, pl. 2, figs. 20–27, text-fig. 4b–c.

*Palmatolepis* aff. *disparilis* Ziegler and Klapper. Plate 115, figs. 25, 31–33, 38, 39 = aff. 1976 *Palmatolepis disparilis* n. sp.—Ziegler and Klapper (in Ziegler *et al.*), p. 119, pl. 1, figs. 18–22, 24–31.

*Remarks:* Several rather deformed specimens lie close to *Pa. disparilis* but differ from it in having a more strongly differentiated lobe and a carina which extends further posteriorward; the basal cavity is developed further anteriorward too.

#### EXPLANATION OF PLATE 109

Figs.  $\times 35$ , unless qualified.

Figs. 1, 8. *Icriodus obliquimarginatus* Bischoff and Ziegler. Gasworks Quarry (GQ210). Oral, lateral views of H10127; juvenile.

Figs. 2–5, 7, 10, 14, 15, 20, 23. *Icriodus expansus* Branson and Mehl group. Figs. 2–5, 7, 10, 14, 15. Middle Devonian morphotypes. Figs. 2, 3 from Gasworks Quarry (GQ20), others from Drake's Island (DI2). 2. Oral view of H10128. 3. Oral view of H10129. 4. Oral view of H10130; young growth stage with discrete nodes. 5. Oral view of H10131; late growth stage with fused nodes. 7, 15. Oral, lateral views of H10132; note prominent anterior denticles and cusp. 10, 14. Lateral, oral views of H10133; note prominent anterior denticles. Figs. 20, 23. Upper Devonian morphotype. Western King (WK5). Lateral and oral views of H10134; note discrete blade denticles.

Figs. 6, 11. *Icriodus latericrescens latericrescens* Branson and Mehl. Oral, oblique lateral views of H10135, Richmond Walk (RW25).

Figs. 9, 12, 13, 16, 18. *Icriodus difficilis* Ziegler and Klapper. Neal Point (NP15). 9, 16. Oral, lateral views of H10136. 13. Oral view of H10137. 12, 18. Lateral, oral view of H10138.

Figs. 17, 22, 24, 26, 32, 34. *Icriodus symmetricus* Branson and Mehl. Fisons Quarry (77c). Figs. 17, 24. Oral, lateral views of H10139. 22, 26. Lateral, oral views of H10140. 32. Oral view of H10141; form with irregular denticulation. 34. Oral view of H10142; juvenile  $\times 65$ .

Fig. 29. *Polygnathus varcus* Stauffer. Oral view of H10154,  $\times 25$ . Mount Wise (MW36).

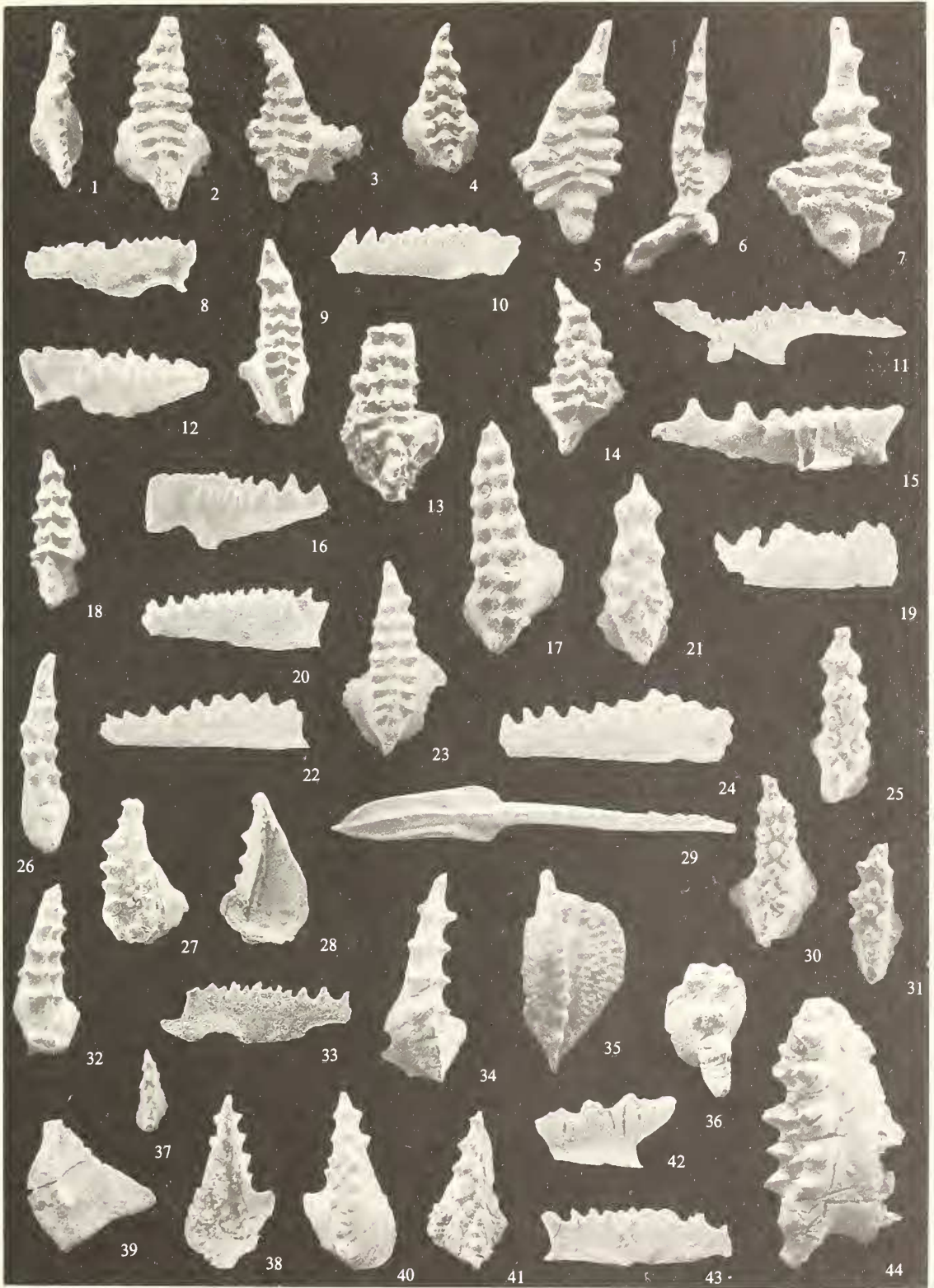
Fig. 35. *Polygnathus asymmetricus* cf. *asymmetricus* Bischoff and Ziegler. Durnford Street (DS1). Oral view of H10155,  $\times 30$ .

Fig. 39. *Palmatolepis* cf. *hassi* Muller and Muller. Durnford Street (DS1). Oral view of H10173,  $\times 30$ .

Figs. 19, 21, 25, 30, 31. *Icriodus* aff. *subterminus* Youngquist. Western King. 19, 25. Lateral, oral views of H10143, (WK1); specimen with high blade. 21. Oral view of H10144, (WK2). 30. Oral view of H10145, (WK2). 31. Oral view of H10146, (WK1); juvenile.

Figs. 27, 28, 33, 36–38, 40–44. *Icriodus alternatus* Branson and Mehl. Western King (WK6a). 27, 28. Oral, aboral views of H10147. 33. Lateral view of H10148. 36, 42. Oral, lateral views of H10149; posterior fragment with strong cusp-like blade like that of *I. cornutus* Sannemann. 37. Oral view of H10150; juvenile. 38, 40. Aboral, oral views of H10151. 41, 43. Oral, lateral views of H10152. 44. Oblique oral view of H10153.





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*Palmatolepis minuta minuta* Branson and Mehl. Plate 115, figs. 10, 17 = 1934 *Palmatolepis minuta* n. sp.—Branson and Mehl, pp. 236–237, pl. 18, figs. 1, 6, 7.

*Palmatolepis subperlobata* Branson and Mehl. Plate 115, fig. 2 = 1934 *Palmatolepis subperlobata* n. sp.—Branson and Mehl, p. 235, pl. 18, figs. 11, 21.

*Palmatolepis subrecta* Miller and Youngquist. Plate 115, figs. 28–30, 34, 40 = 1947 *Palmatolepis subrecta* n. sp.—Miller and Youngquist, pp. 513–514, pl. 75, figs. 7–11.

*Palmatolepis* aff. *subrecta* Miller and Youngquist. Plate 115, fig. 35.

*Remarks:* A few specimens from Durnford Street are characterized by a carina which terminates at theazygous node. The platform shape is consistent with that of *Pa. subrecta*.

*Palmatolepis termini* Sannemann. Plate 115, figs. 36, 37 = 1955 *Palmatolepis termini* n. sp.—Sannemann, p. 149, pl. 1, figs. 1–3.

*Palmatolepis triangularis* Sannemann. Plate 115, figs. 1, 3–5, 8, 14 = 1955 *Palmatolepis triangularis* n. sp.—Sannemann, pp. 327–328, pl. 24, fig. 3.

*Polygnathus angustipennatus* Bischoff and Ziegler, *sensu lato*. Plate 108, figs. 6, 10, 14 = 1957 *Polygnathus angustipennatus* n. sp.—Bischoff and Ziegler, p. 85, pl. 2, fig. 16; pl. 3, figs. 1–3.

*Remarks:* The author is in agreement with Klapper (1971) in considering that some of the forms assigned to the *Po. robusticostatus* group would fall into synonymy in a broader concept of intraspecific variation. Similarly, it is probable that the ontogeny of an individual involves more than one of the morphotypes in the group. Only four specimens of the *Po. robusticostatus* group have been found in the Plymouth Limestone, and although they are not well preserved each is unique in some respect. These are referred to *Po. angustipennatus s.l.*, herein considered to embrace those members of the group with a distinct platform development and a carina which clearly extends posterior of the platform. The high anterior blade denticles have been cited as a distinguishing character of *Po. angustipennatus s.s.*, however some specimens assigned to *Po. angusticostatus* (e.g. Orr 1971, pl. 4, figs. 12–14) also have such a blade.

#### EXPLANATION OF PLATE 110

Figs.  $\times 20$ , unless qualified.

Figs. 1, 2, 4, 7, 12, 13. *Polygnathus latus* Wittekindt. 1, 2. Oral, oblique—posterior views of H10156, Gasworks Quarry (GQ20). 4, 7. Oral, lateral views of H10157, Neal Point (NP2). 12, 13. Oral, aboral views of H10158,  $\times 35$ , Neal Point (NP2).

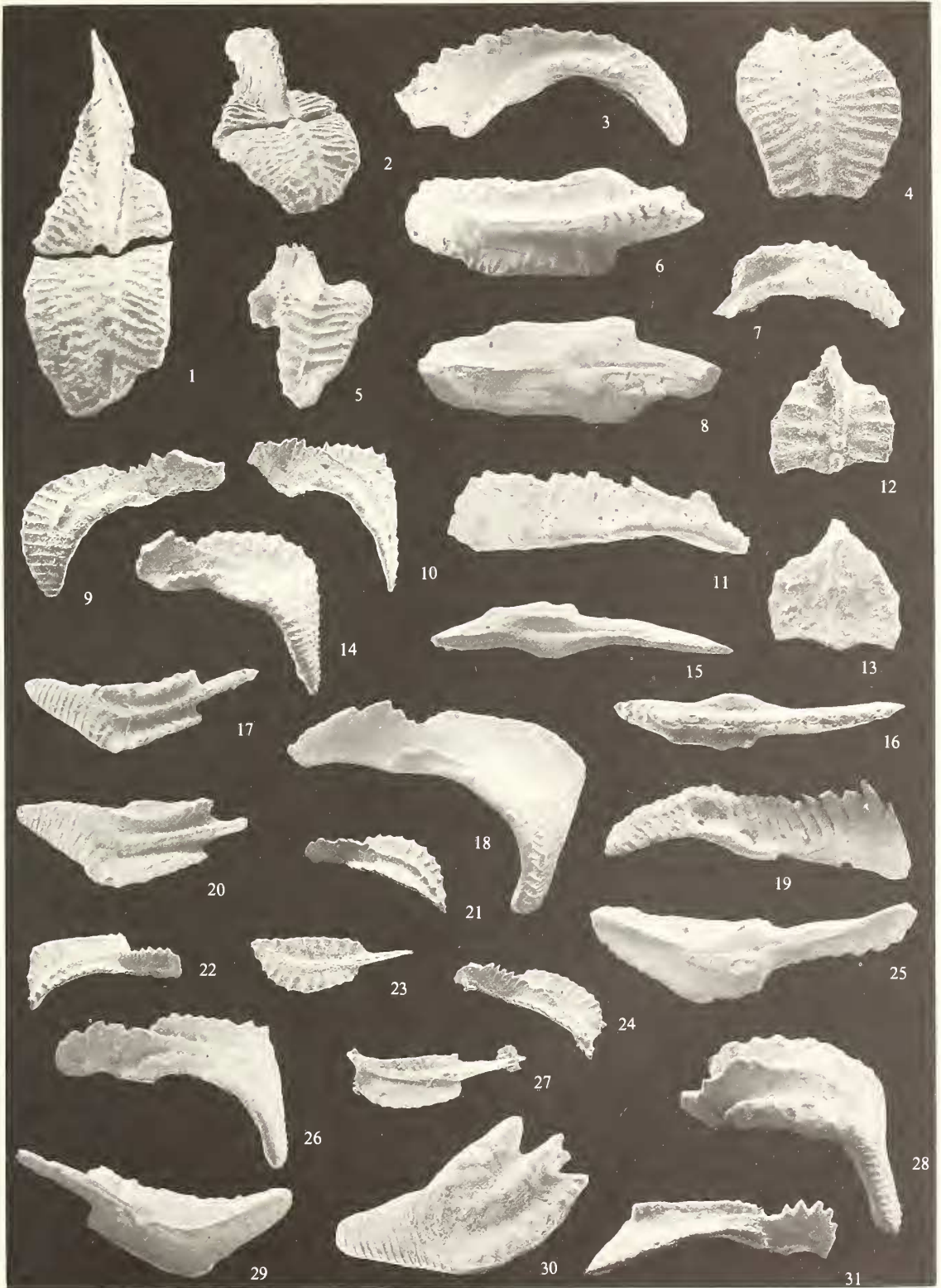
Figs. 3, 5, 6, 8, 11, 15, 16, 19, 25. *Polygnathus* aff. *variabilis* Bischoff and Ziegler. 3, 5, 6, 8. Inner lateral, posterior, oral, aboral views of H10159, Gasworks Quarry (GW20). 11, 15, 16. Inner lateral, aboral, oral views of H10160, Princerock Quarry (PS4). 19, 25. Inner lateral, aboral views of H10161, Gasworks Quarry (GQ20).

Figs. 9, 10, 28, 30. *Polygnathus linguiformis* Hinde, ?delta morphotype Ziegler and Klapper. Specimens with distinct tongues. From Richmond Walk (RW28). 9. Latero-oral view of H10162; specimen with short tongue. 10. Latero-oral view of H10163; specimen with incipient carina. 28, 30. Latero-oral, postero-oral views of H10164; late growth stage showing affinity with epsilon morphotype.

Figs. 14, 17, 20, 26, 29. *Polygnathus linguiformis* Hinde, epsilon morphotype Ziegler and Klapper. From Mutton Cove (MC32). 14, 20. Latero-oral, oral views of H10165. 17. Oral view of H10166. 26, 29. Latero-oral, aboral views of H10167; note relatively large basal cavity and anterior furrowing.

Figs. 18, 22, 24, 27, 31. *Polygnathus linguiformis linguiformis* Hinde. 18. Latero-oral view of H10168, Mount Wise (MW36). 22. Latero-oral view of H10169,  $\times 35$ , Botus Fleming (BF3); juvenile. 24, 27. Latero-oral views of H10170,  $\times 35$ , Botus Fleming (BF3); juvenile. Fig. 31. Lateral view of H10172; atypically slender specimen with unusual blade. Gasworks Quarry (GQ20).

Figs. 21, 23. *Polygnathus linguiformis* Hinde, delta morphotype Ziegler and Klapper. Botus Fleming (BF3). Latero-oral views of H10171,  $\times 35$ . Note single transverse ridge on posterior platform.



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*Polygnathus ansatus* Ziegler and Klapper. Plate 112, figs. 1-3, 5, 6, 8-12, 16, 19-24, 26, 27, 29-31, 33, 34, 36-38 = 1976 *Polygnathus ansatus* n. sp.—Ziegler and Klapper (in Ziegler *et al.*), pp. 119-120, pl. 2, figs. 11-26.

*Remarks:* The species is represented by numerous specimens at Mount Wise, and the variability exhibited by the fauna (see Plate 112) is most pronounced. As discussed below (see *Po. varcus* group), several morphological features used as a basis for discrimination of species of the *varcus* group cannot, in the authors experience, be applied strictly. The criterion used here in separating the polygnathids is the relative width of the platform (including the anterior part), this being comparatively broader in *Po. ansatus* than in other members of the *varcus* group. The division is nevertheless rather difficult to apply at Mount Wise, and the possibility exists that specimens from that fauna referred to *Po. timorensis* and *Po. varcus* are intraspecific variants of one natural species.

*Polygnathus asymmetricus* Bischoff and Ziegler group.

*Remarks:* Three subspecies are herein recognized. *Po. a. asymmetricus* is characterized by a platform which is often subquadrate in outline and bears a minute pit aborally. *Po. a. ovalis* has an oval platform and a relatively larger, symmetrical basal cavity. *Po. a. n. subsp. A* has a distinctly asymmetrical basal cavity and the platform outline reflects this.

*Polygnathus asymmetricus asymmetricus* Bischoff and Ziegler. Plate 109, fig. 35 = 1957 *Polygnathus dubia asymmetrica* n. subsp.—Bischoff and Ziegler, pp. 88-89, pl. 16, figs. 18, 20-22; pl. 21, fig. 3.

*Remarks:* One specimen referred by Ziegler (1958, pl. 1, figs. 3a-b) to *Po. dubia dubia* = *Po. a. ovalis* bears a minute pit identical to that of associated specimens of *Po. a. asymmetricus* (e.g. *op. cit.*, pl. 1, fig. 10), but quite unlike those others referred to *Po. a. ovalis*.

*Polygnathus asymmetricus ovalis* Ziegler and Klapper. Plate 115, figs. 15, 22, 42, 43; 241, 44 = 1964 *Polygnathus asymmetricus ovalis* subsp. nov.—Ziegler and Klapper (in Ziegler *et al.*), pp. 422-423.

#### EXPLANATION OF PLATE 111

All figs.  $\times 20$ .

Figs. 1, 6, 29, 30, 32. Ramiform elements from the Gasworks Quarry (GQ20) and Princerock Quarry (PS4; fig. 6 only). Lateral views of: 1. H10174, ?A<sub>2</sub> element. 6. H10175, A<sub>2</sub> element. 29. H10202, B<sub>1</sub> element. 30. H10203, B<sub>1</sub> element. 32. Oral view of H10204, ?B<sub>2</sub> element.

Figs. 2-4. Lonchodiniiform element. Gasworks Quarry (GQ20). Anterio-oral, latero-oral views of H10176, ?B<sub>2</sub> element of *Polygnathus* (= *Parapolygnathus*) *variabilis*.

Fig. 5. Ozarkodiniiform, O<sub>1</sub> element. Princerock Quarry (PS4). Lateral view of H10177.

Figs. 7, 16. Trichonodelliform A<sub>3</sub> element. Teats Hill Quarry (TH44/3). Posterior, aboral views of H10178.

Figs. 8, 12, 18. Type 2 (*sensu* Klapper and Philip 1971) elements from Richmond Walk (RW28). 8. Lateral view of H10179, B<sub>2</sub> element. 12. Lateral view of H10180, N element. 18. Latero-aboral view of H10181, O<sub>2</sub> element. Possible multielement association (*partim*).

Figs. 9, 13, 17. *Spathognathodus planus*. Mount Wise (MW36). Lateral views of: 9. H10182. 13. H10183. 17. H10184, ?O<sub>1</sub> elements of *Polygnathus varcus* s.l.

Figs. 10, 11, 19, 22, 23, 25, 26, 33, 34, 37, 38. Type 1 (*sensu* Klapper and Philip 1971) elements from Mount Wise (MW36) and Richmond Walk (RW28; fig. 22 only). 10. Posterior view of H10185, A<sub>3</sub> element.

11. Lateral view of H10187, N element. 19. Lateral view of H10194, O<sub>1</sub> element. 22. Lateral view of H10195, A<sub>1</sub> element. 23. Lateral view of H10196, A<sub>1</sub> element. 25. Posterior view of H10197, A<sub>2</sub> element. 26. Lateral view of H10306, A<sub>1</sub> element. 33, 34. Lateral, oral views of H10198, A<sub>2</sub> element. 37, 38. Oral, lateral views of H10186, A<sub>3</sub> element. ?Elements from two multielement associations (*partim*).

Figs. 14, 20, 21, 24, 27, 28, 31, 35, 36. Type 2 elements from Mount Wise (MW36). 14. Lateral view of H10188, N element. 20, 21. Lateral, oral views of H10189, O<sub>2</sub> element. 24. Lateral view of H10190, ?B<sub>1</sub> element. 27. Lateral view of H10199, B<sub>1</sub> element. 28. Lateral view of H10200, B<sub>2</sub> element. 31. Lateral view of H10191, B<sub>2</sub> element. 35. Posterior view of H10192, B<sub>3</sub> element. 36. Posterior view of H10201, B<sub>3</sub> element. ?Elements from two multielement associations (*partim*).

Fig. 15. Bryantodontiform element. Richmond Walk (RW25). Lateral view of H10193. ?Multielement associate of '*Polygnathellus*' (Plate 113, figs. 30, 31).





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*Polygnathus asymmetricus* subsp. A nov.

Plate 115, figs. 18, 19

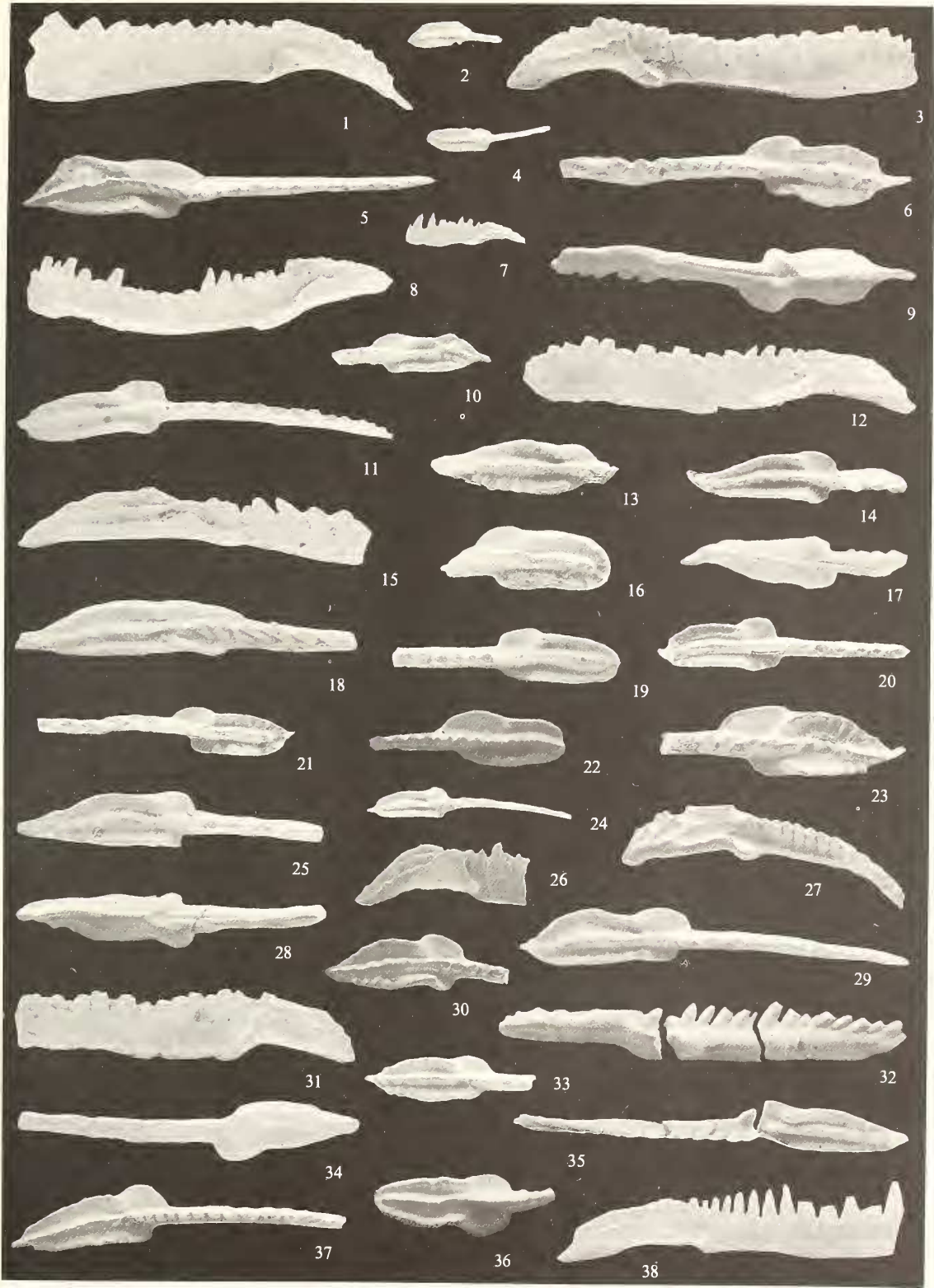
- p. 1949 *Polygnathus dubia* Hinde—Beckmann, pp. 154–155, pl. 4, fig. 4.  
 p. 1966 *Polygnathus asymmetrica asymmetrica* Bischoff and Ziegler—Flajs, pp. 230–232, pl. 26, figs. 4–6.  
 . 1968 *Polygnathus* n. sp. c—Pollock, p. 438, pl. 62, figs. 28, 29, 35.  
 . 1970 *Polygnathus asymmetricus asymmetricus* Bischoff and Ziegler—Seddon, pl. 10, figs. 2a, b.  
 p. 1974 *Polygnathus asymmetricus*—Mouravieff, in Bouckaert and Streel, F, p. 2.

*Description:* The unit is slightly to strongly asymmetric in plan view and slightly to moderately arched in lateral view. The blade is fairly deep and short, about one fifth of the total unit length, and consists of three-five, mostly fused denticles which tend to increase in height anteriorward. The carina becomes progressively lower posteriorward in conjunction with the broadening of the denticles into fused nodes which attain their maximum development a little posterior of platform midlength where there are two nodes invariably larger than all others. Posterior of that point, the carina is represented by two or three discrete, small and increasingly separated nodes. In some specimens (about half) the carina is slightly sigmoidal and has an arcuate trend (the concave side is outward) a little anterior of platform midlength. Adjacent to this arc, the outer platform is slightly depressed. This position also marks the greatest width of the unit and there may be strong lateral growth. Thus the outer platform is invariably broader than the inner, the difference being particularly pronounced in juveniles. Posteriorward, the platform tapers evenly to a point, while anteriorward the platform margins are smoothly rounded and stretched downward to meet the blade at approximately opposite points. The oral surface bears fine granules which may become fused into ridges marginally and anteriorward, particularly in larger specimens. The ornament on the inner and outer sides is not always the same. Aborally, the unit has a large asymmetrical basal-cavity, the centre of which is situated at platform mid-length. The shape of the cavity is approximately triangular. It is strongly expanded laterally at the anterior end, extending in the direction of maximum development of the outer platform. Posteriorward, the expanded side of the cavity tapers irregularly towards a point one quarter, or less, of the total platform length from the posterior tip in such a way as a fold is often developed. The margin of the cavity on the inner side is arcuate. The depression on the oral surface of the outer platform corresponds to a position immediately anterior of the basal cavity. The keel is grooved anteriorward under the blade.

## EXPLANATION OF PLATE 112

All figs.  $\times 25$ . All from Mount Wise (MW36).

- Figs. 1–38. The *Polygnathus varcus* Stauffer group. Specimens show variation in platform ornament and anterior trough development within a single fauna. Most specimens have incomplete blades.  
 Figs. 1, 3, 5, 6, 8–12, 16, 19–24, 26, 27, 29–31, 33, 34, 36–38; ?2, 4, 7. *Polygnathus ansatus* Ziegler and Klapper. Figs. 1, 6, 9. Lateral, oral, aboral views of H10205. 3, 5. Lateral, oral views of H10207; specimen with adcarinal node. 8, 11. Lateral, oral views of H10209; near symmetrical development of anterior platform. 10. Oral view of H10210; specimen with adcarinal nodes and ridges. 12, 29. Lateral, oral views of H10211. 16. Oral view of H10215; specimen with rounded posterior platform and short carina. 19. Oral view of H10216; as 16. 20. Oral view of H10217. 21. Oral view of H10218. 22. Oral view of H10219; as 16, and strong denticles at inner geniculation point. 23. Oral view of H10200; specimen with strong marginal ridges. 24. Oral view of H10221; relatively small specimen with near symmetrical anterior platform development as in *Po. varcus* s.s. (cf. fig. 11). 26, 30. Lateral, oral views of H10223, specimen with high inner geniculation point. 27. Latero-oral view of H10224; extreme development of platform ornament. 31, 34. Lateral, aboral views of H10225. 33. Oral view of H10227. 36. Oral view of H10228. 37, 38. Oral, lateral views of H10229. Figs. 2, 4, 7. Very small growth stages of uncertain affinity. 2. Oral view of H10206. 4, 7. Oral, lateral views of H10208.  
 Figs. 13, 14, 15, 17, 18, 25, 28, 32, 35. *Polygnathus timorensis* Klapper, Philip and Jackson. 13. Oral view of H10212. 14, 17. Oral, aboral views of H10213. 15, 18. Lateral, oral views of H10214; large elongate specimen with posteriorly inclined blade denticles (cf. fig. 32). 25, 28. Oral, aboral views of H10222; relatively large specimen close to holotype. 32, 35. Lateral, oral views of H10226; specimen with anteriorly inclined blade denticles.



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*Remarks:* The above description is based largely on well preserved material from Nismes in Belgium loaned to the author by Dr. N. Mouravieff. *Po. a.* subsp. A differs from other subspecies principally in the larger and strongly asymmetrical basal cavity. *Pa. ? disparalvea* differs in bearing a well developed lobe, a coarser ornament and by the extreme development of the basal cavity which also lies relatively further to the posterior than in the new subspecies. *Pa. disparilis* is similar but is generally more robust, bears a coarser ornament, has a shorter carina, a more variable anterior platform development, and a more strongly expanded basal cavity.

*Polygnathus cristatus* Hinde. Plate 115, fig. 23 = 1879 *Polygnathus cristatus* n. sp.—Hinde, p. 366, pl. 17, fig. 11.

*Polygnathus dengleri* Bischoff and Ziegler. Plate 115, figs. 20, 21, 24 = 1957 *Polygnathus dengleri* n. sp.—Bischoff and Ziegler, pp. 87–88, pl. 15, figs. 14, 15, 17–24; pl. 16, figs. 1–4.

*Polygnathus* aff. *latifossatus* Wirth. Plate 108, figs. 19, 20, 33, 36 = aff. 1967 *Polygnathus latifossatus* n. sp.—Wirth, pp. 227–228, pl. 22, figs. 17–19.

*Remarks:* Two specimens from Richmond Walk share the particular characteristic of an inturned posterior tip. One appears to lie close to *Po. latifossatus*, but adhering basal plate obscures the basal cavity, the form of which is a diagnostic feature of *Po. latifossatus*. A second specimen (Plate 108, figs. 33, 36) has a much reduced, asymmetrically developed platform and a conspicuously high carina. This association is reminiscent of the intergrading couple *Po. latifossatus*—*S. semialternans* (see Wirth 1967, fig. 14).

*Polygnathus latus* Wittekindt. Plate 110, figs. 1, 2, 4, 7, 12, 13 = 1966 *Polygnathus lata* n. sp.—Wittekindt, p. 635, pl. 2, figs. 6, 8, 9.

*Remarks:* Only three specimens have been found but these display a close similarity to the types, particularly as regards the broad flat platform. Ziegler and Klapper (1976, p. 123) have discussed the resemblance of this species to the delta morphotype of *Po. linguiformis*. The two forms differ in the position of the maximum platform width.

#### EXPLANATION OF PLATE 113

Figs.  $\times 20$ , unless qualified.

Figs. 1–4. *Polygnathus tuberculatus* Hinde. Mount Wise (MW36). 1, 2, 3. Oral, aboral, oblique-lateral views of H10230. 4. Lateral-oral view of H10231.

Figs. 5, 8, 9, 13, 16, 21, 28. *Polygnathus* aff. *tuberculatus* Hinde. Mount Wise (MW36). 5, 8. Oral, latero-oral views of H10234. 9, 13, 16. Lateral, oral, aboral views of H10241; specimen with incipient carina on tongue. 21. Oral view of H10232; juvenile. 28. Oral view of H10233; specimen with one rostral ridge and posterior carina.

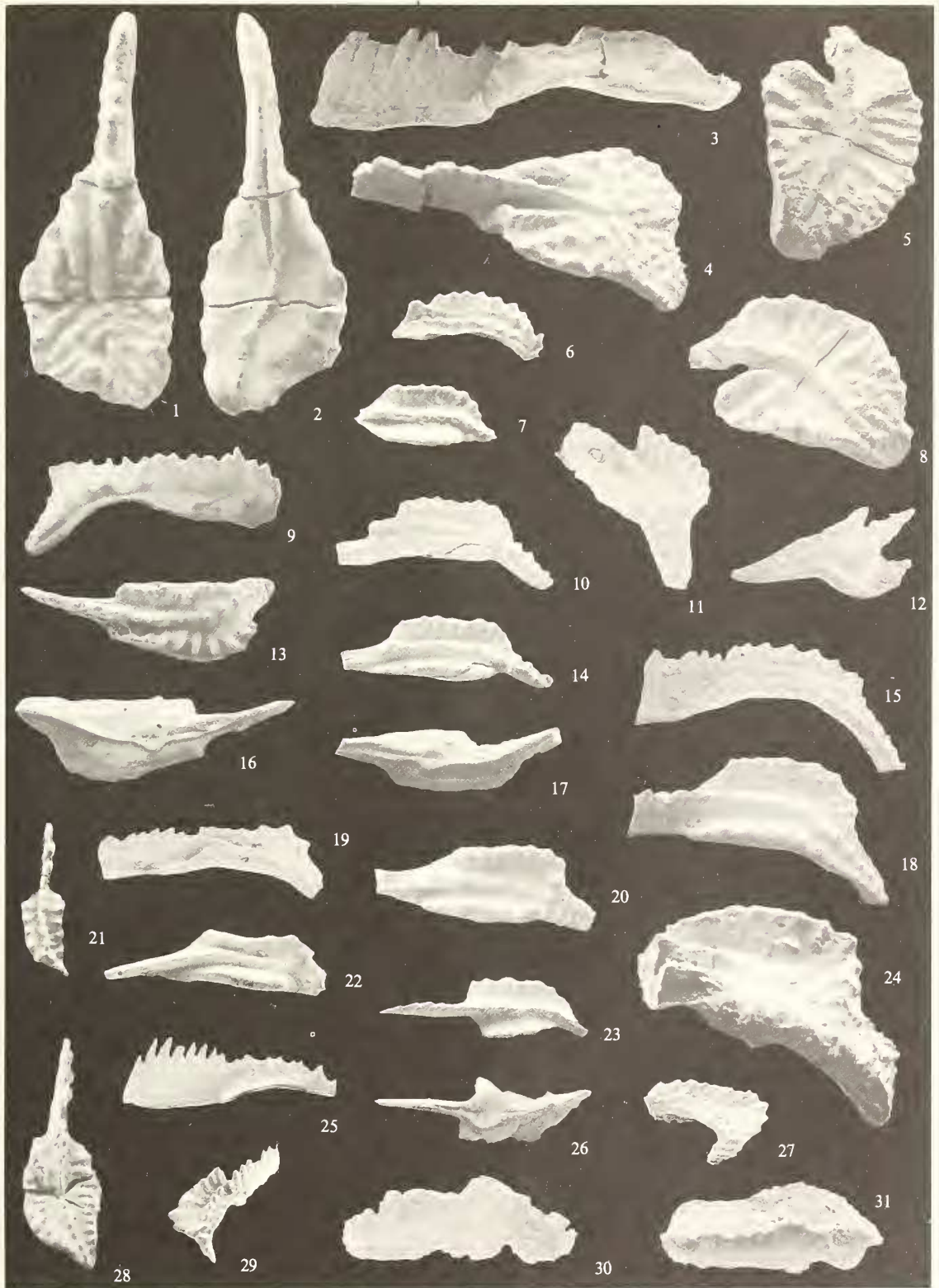
Figs. 6, 7, 10–12, 14, 15, 17–20, 22, 24. *Polygnathus linguiformis mucronatus* Wittekindt. Mount Wise (MW36). 6, 7. Lateral, oral views of H10235. 10, 14, 17. Latero-oral, oral, aboral views of H10236; specimen with incipient posterior carina. 11, 20. Posterio-oral, oral views of H10237; specimen with no posterior carina. 12, 15, 18. Posterior, lateral, latero-oral views of H10238; specimen with posterior carina. 19, 22. Lateral, oral views of H10239; atypical specimen with thick platform margins. 24. Latero-oral view of H10240; late growth stage continues to exhibit constricted tongue and rounded outer posterior platform margin.

Figs. 23, 25, 26. *Polygnathus* aff. *porcillus* Stauffer. Richmond Walk (RW39). Oral, lateral, aboral views of H10242.

Figs. 27, 29. *Polygnathus linguiformis* Hinde, *?epsilon* morphotype Ziegler and Klapper. 27. Latero-oral view of H10243,  $\times 25$ , Princeroock Quarry (PS3). 29. Posterio-oral view of H10244,  $\times 30$ , Gasworks Quarry (GW20).

Figs. 30, 31. *Polygnathellus* sp. Richmond Walk (RW25). Lateral, oral views of H10245.





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*Polygnathus linguiformis* Hinde group.

*Remarks:* *Po. linguiformis*, as conceived at present, is a very broad species, although Hinde's original definition does not embrace all the variants so far recognized; the latter are therefore considered collectively as the *Po. linguiformis* group.

The *Po. linguiformis* group is here defined as including relatively elongate polygnathids in which the posterior part of the platform, or tongue (see Bultynck 1970, p. 126, footnote 1), is bent downwards and inwards, and bears transverse ridges and/or a carina; aborally, there is a small basal cavity situated in the anterior half of the platform. Thus defined, the group includes all the subspecies and morphotypes hitherto recognized (see Wittekindt 1966, Bultynck 1970, Klapper 1971, Ziegler *et al.* 1976).

Representatives of the *Po. linguiformis* group are common in the Plymouth Limestone. The majority of them correspond to the gamma morphotype of Bultynck (1970), herein referred to *Po. l. linguiformis* (*q.v.*). Ziegler *et al.* (1976) have recently referred subspecies of *Po. linguiformis* to morphotypic level, but it is the author's opinion that it is more appropriate to regard established morphotypes as subspecies of *Po. linguiformis*.

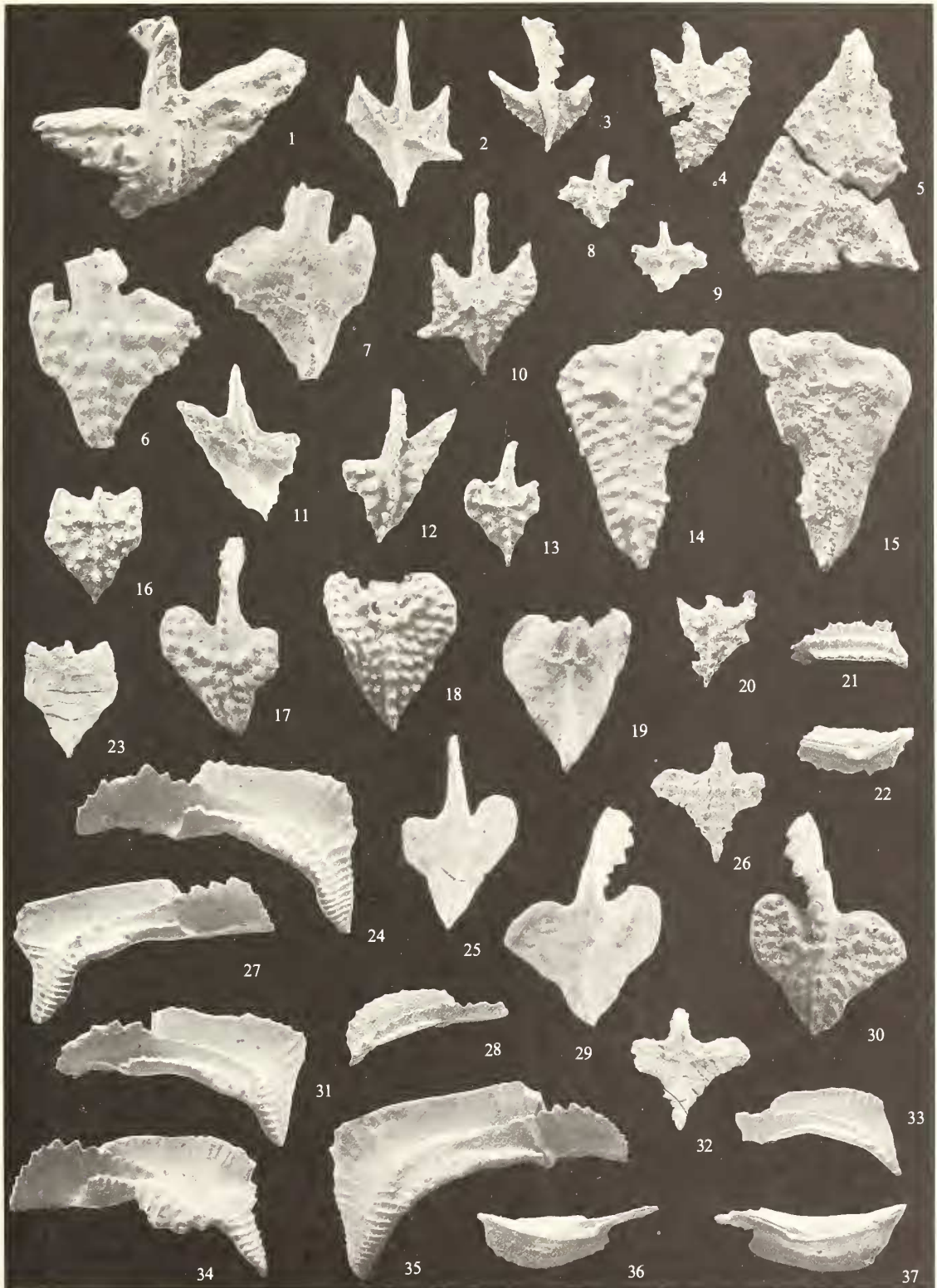
delta morphotype Ziegler and Klapper. Plate 110, figs. 21, 23; 29, 10, 28, 30 = 1976 *Polygnathus linguiformis linguiformis* Hinde delta morphotype nov.—Ziegler and Klapper (*in* Ziegler *et al.*), p. 123, pl. 4, figs. 4–8.

*Remarks:* A single specimen from East Cornwall corresponds exactly to this morphotype which is characterized by a comparatively flat platform with an arcuate outer margin. There is no tongue development in this, or in the specimens illustrated by Ziegler and Klapper (1976) but all these are relatively small and the somewhat larger specimen figured by Wittekindt (1966, pl. 2, fig. 11) bears only a weak carina posteriorly. A specimen figured by Klapper (1971, pl. 3, figs. 13–14) has an evenly curved outer margin too, although it differs in bearing a short tongue; it also comes from a lower stratigraphical level. A few specimens from Richmond Walk also have a tongue development and are questionably placed here on the basis of their evenly curved outer margins and relatively flat platforms. It seems reasonable to suppose that later growth stages of the delta morphotype might bear such a tongue.

#### EXPLANATION OF PLATE 114

Various magnifications.

- Figs. 1, 11, 12. *Ancyrodella* aff. *gigas* Youngquist. Durnford Street (DS1). 1. Oral view of H10246,  $\times 25$ . 11, 12. Aboral, oral views of H10247,  $\times 35$ . Specimens sheared.
- Figs. 2, 8–10, 20. *Ancyrodella curvatus* (Branson and Mehl). 2, 10. Aboral, oral views of H10248,  $\times 30$ . Western King (WKB1). 8, 9. Oral, aboral views of H10249,  $\times 70$ , Fisons Quarry (FQ77); juvenile. 20. Oral view of H10250,  $\times 70$ , Fisons Quarry (FQ77c).
- Fig. 3. *Ancyrodella nodosa* Ulrich and Bassler. Western King (WK56H). Oral view of H10251,  $\times 40$ .
- Fig. 4. *Ancyrodella gigas* Youngquist. Wilderness Point (C135). Oral view of H10252,  $\times 35$ .
- Fig. 5. *Ancyrognathus triangularis* Youngquist. Fisons Quarry (FQ77). Oral view of H10253,  $\times 25$ .
- Figs. 6, 7. *Ancyrodella* aff. *rugosa* Branson and Mehl. Western King (WK2). Oral, aboral views of H10254,  $\times 25$ ; one lobe broken.
- Figs. 13, 16–19, 23, 25, 26, 29, 30, 32. *Ancyrodella rotundiloba alata* Glenister and Klapper. Western King. 13. Oral view of H10255, (WK1),  $\times 40$ ; juvenile. 16, 23. Oral, aboral views of H10256, (WK1),  $\times 40$ ; atypically, little secondary keel development. 17, 25. Oral, aboral views of H10257, (WK2),  $\times 25$ . 18, 19. Oral, aboral views of H10258, (WK2),  $\times 25$ ; platform margins turned upward. 26, 32. Oral, aboral views of H10259, (WK2),  $\times 45$ ; juvenile. 29, 30. Aboral, oral views of H10260, (WK1),  $\times 25$ .
- Figs. 14, 15. *Ancyrodella rotundiloba* (Bryant). Radford Quarry (R117). Oral, aboral views of H10261,  $\times 25$ .
- Figs. 21, 22. *Ancyrognathus cryptus* Ziegler. Western King (WKB2). Oblique-oral, aboral views of H10262,  $\times 40$ .
- Figs. 24, 27, 28, 31, 33–37. *Polygnathus linguiformis linguiformis* Hinde. Mount Wise (MW36). Inner latero-oral and aboral views of: 24. H10263,  $\times 20$ . 27. H10264,  $\times 20$ . 28, 36. H10269,  $\times 40$ ; juvenile. 31. H10265,  $\times 20$ . 34. H10266,  $\times 25$ ; unusual specimen with strongly expanded inner posterior edge. 35. H10267,  $\times 25$ . 33, 36. H10268,  $\times 25$ ; juvenile.



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## epsilon morphotype Ziegler and Klapper

Plate 110, figs. 14, 17, 20, 26, 29; ?Plate 113, figs. 27, 29

- p. 1956 *Polygnathus linguiformis* Hinde—Ziegler, pp. 103–104, pl. 7, figs. 15–18.  
 p. 1957 *Polygnathus linguiformis* Hinde—Bischoff and Ziegler, pp. 92–93, pl. 1, fig. 4; pl. 16, figs. 32, 33;  
 pl. 17, figs. 5, 6.  
 1966 *Polygnathus linguiformis* Hinde—Ziegler, pl. 1, figs. 8, 9.  
 1976 *Polygnathus linguiformis linguiformis* Hinde epsilon morphotype—Ziegler and Klapper (*in*  
*Ziegler et al.*), pp. 123–124, pl. 4, figs. 3, 12, 14, 24.

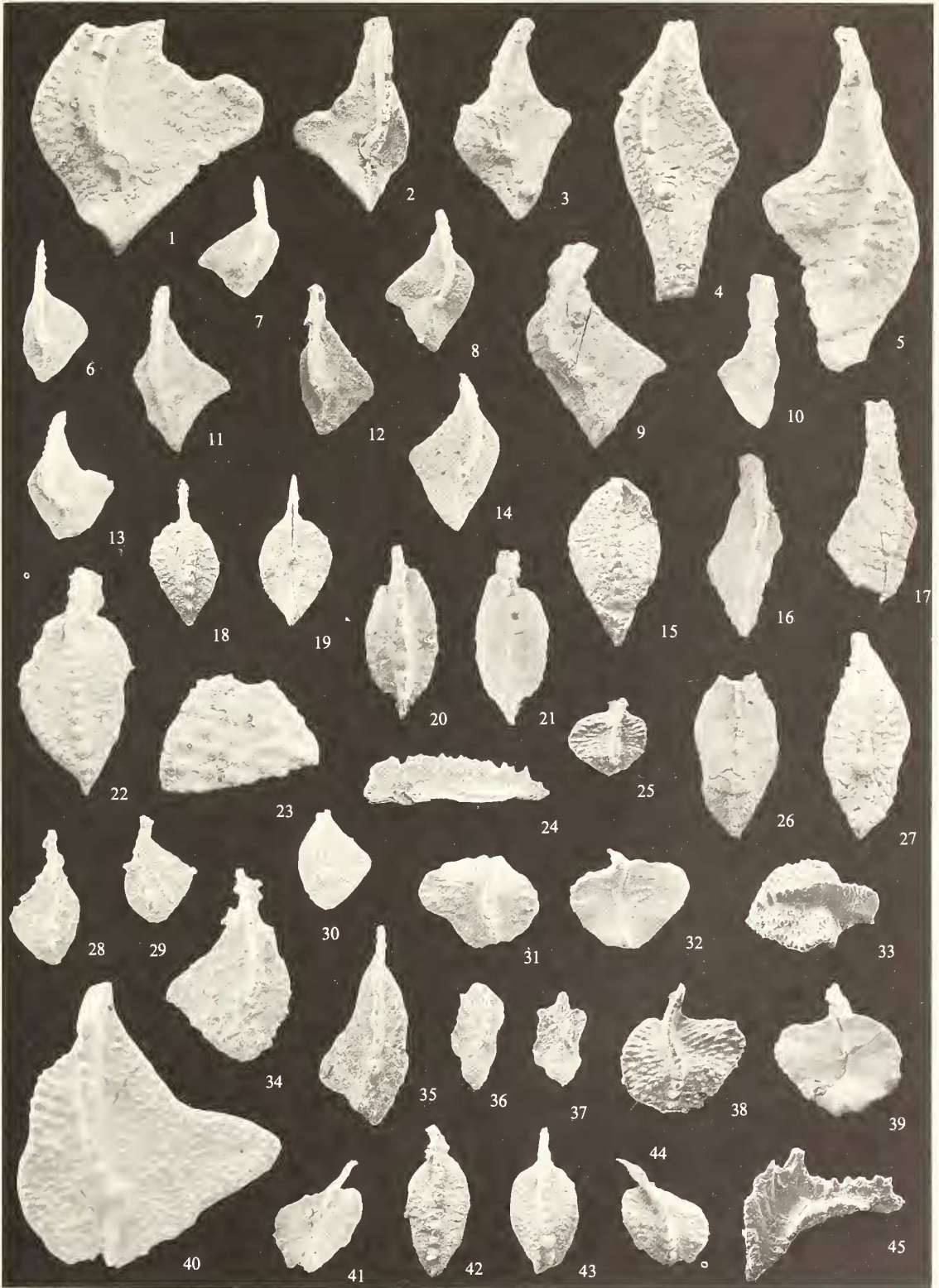
*Remarks:* A few small specimens questionably included here may be juvenile forms of this morphotype, but typical representatives are not found in association. The relationship of these small forms to *Po. dobrogensis* Mirauta 1971 is not clear, but they are superficially similar. In the Plymouth specimens of the epsilon morphotype, the basal cavity is slightly larger than in specimens of *Po. l. linguiformis*, and there is also a greater degree of anterior furrowing. *Po. l. mucronatus* has coarser marginal ornament and a more strongly inturred posterior outer platform margin than the epsilon morphotype; it also lacks the rostral ridges parallel to the carina.

## EXPLANATION OF PLATE 115

Figs.  $\times 30$ , unless qualified.

- Figs. 1, 3, 5, 8, 14, ?4. *Palmatolepis triangularis* Sannemann. Western King. Oral views of: 1. H10270, (WK6b1). 3. H10271, (WK6a). 4. H10272, (WK6a); atypically elongate specimen. 5. H10273, (WK6a). 8. H10274, (WK6a). 14. H10275, (WK6a).  
 Fig. 2. *Palmatolepis subperlobata* Branson and Mehl. Oral view of H10276, Western King (WK6a).  
 Figs. 6, 7, 12, 13. *Palmatolepis delicatula delicatula* Branson and Mehl. Western King. Oral views of: 6. H10277, (WKb1). 7. H10278, (WKb2). 12. H10279, (WKb2). 13. H10280, (WKb2).  
 Figs. 9, 11. *Palmatolepis delicatula clarki* Ziegler. Western King. Oral views of: 9. H10281, (WKb1); large specimen, close to *Pa. subperlobata*. 11. H10282, (WKb2).  
 Figs. 10, 17. *Palmatolepis minuta minuta* Branson and Mehl. Western King. Oral views of: 10. H10283, (WKb1). 17. H10305, (WKb1).  
 Figs. 15, 22, 42, 43, ?41, 44. *Polygnathus asymmetricus ovalis* Ziegler and Klapper. From Western King, except 41, 44. 15. Oral view of H10284, (WK1). 22. Oral view of H10285, (WK2). 42. Oral view of H10287, (WK1). 43. Oral view of H10288, (WK1). 41, 44. Aboral, oral views of H10286, Durnford Street (DS1); deformed specimen.  
 Fig. 16. *Palmatolepis* cf. *tenuipunctata* Sannemann. Western King (WKb1). Oral view of H10289.  
 Figs. 18, 19. *Polygnathus asymmetricus* subsp. A nov. Durnford Street (DS1). Oral, aboral views of H10290.  
 Figs. 20, 21, 24. *Polygnathus dengleri* Bischoff and Ziegler. Western King (WK2). Oral, aboral, lateral views of H10291.  
 Fig. 23. *Polygnathus cristatus* Hinde. West Hoe (H1). Oral view of anterior platform fragment H10292.  
 Figs. 25, 31–33, 38, 39. *Palmatolepis* aff. *disparilis* Ziegler and Klapper. Durnford Street (DS1); specimens deformed. 25. Oral view of H10293; juvenile. 31, 32. Oral, aboral views of H10294,  $\times 40$ . 33, 38, 39. Latero-oral, oral, aboral views of H10295.  
 Figs. 26, 27. *Palmatolepis* cf. *disparilis* Ziegler and Klapper. Aboral, oral views of H10296, West Hoe (H1); adhering dolomite gives the appearance of an azygous node.  
 Figs. 28–30, 34, 40. *Palmatolepis subrecta* Miller and Youngquist. Fisons Quarry (77b). Oral views of growth series; 28. H10297. 29. H10298. 30. H10299,  $\times 35$ . 34. H10300. 40. H10301; latest stage shows affinities to *Pa. hassi*.  
 Fig. 35. *Palmatolepis* aff. *subrecta* Miller and Youngquist. Durnford Street (DS1). Oral view of H10302; specimen has been laterally compressed.  
 Figs. 36, 37. *Palmatolepis termini* Sannemann. Radford Quarry (R119). Oral, oblique posterior views of H10303.  
 Fig. 45. Nothognathelliform element. Wilderness Point (C135/6). Lateral view of H10304,  $\times 25$ .





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*Polygnathus linguiformis linguiformis* Hinde

Plate 110, figs. 18, 22, 24, 27; Plate 114, figs. 24, 27, 28, 31, 33-37

- 1879 *Polygnathus linguiformis* n. sp.—Hinde, p. 367, pl. 17, fig. 15.  
 p. 1966 *Polygnathus linguiformis linguiformis* Hinde—Wittekindt, pp. 635-6, pl. 2, fig. 10.  
 . 1970 *Polygnathus linguiformis linguiformis* Hinde gamma morphotype nov.—Bultynck, pp. 126-127, pl. 11, figs. 1-3, 6; pl. 12, figs. 2, 3, 5.

*Remarks:* The gamma morphotype of Bultynck and the type of *Po. linguiformis* are regarded as one and the same, and is here called *Po. l. linguiformis*. This subspecies nevertheless embraces a wide range of variation, but 'adult' specimens with flattened platforms, outer borders evenly curved throughout, a posterior carina or bearing coarse ribs are excluded since they do not occur at Mount Wise. Small specimens of this form are characterized by a very small or absent tongue development and consequently a carina which extends to the posterior end of the unit. Furthermore, the inner platform is strongly reduced, and the basal cavity is relatively large and situated near the anterior end of the platform. Even at this early growth stage, there appears to be some variation in the development of the posterior platform (cf. Plate 110, figs. 22, 24).

*Polygnathus linguiformis mucronatus* Wittekindt

Plate 113, figs. 6, 7, 10-12, 14, 15, 17-20, 22, 24

- p. 1957 *Polygnathus linguiformis* Hinde—Bischoff and Ziegler, p. 100, pl. 17, fig. 8.  
 1966 *Polygnathus linguiformis mucronata* n. subsp.—Wittekindt, p. 636, pl. 2, figs. 13, 15.  
 . 1967 *Polygnathus linguiformis mucronata* Wittekindt—Adrichem-Boogaert, p. 184, pl. 3, fig. 2.  
 ?p. 1967 *Polygnathus linguiformis* ssp.—Wirth, p. 229, pl. 21, fig. 26, pl. 22, fig. 2.  
 . 1976 *Polygnathus linguiformis linguiformis* Hinde zeta morphotype—Ziegler and Klapper (*in* Ziegler *et al.*), p. 124, pl. 4, figs. 20, 21 (see synonymy).

*Diagnosis* (revised): A rather robust linguiform polygnathid bearing coarse marginal ornament separated from the carina by narrow adcarinal grooves. The tongue is abruptly constricted and, in juveniles, strongly reduced; it may or may not bear a carina.

*Description:* The platform is thick and the margins upturned. From the steep and strongly serrate margins, coarse ridges extend perpendicularly to near the carina from which they are separated by narrow adcarinal grooves. The outer platform is both wider and longer than the inner platform but both sides are otherwise similar in development. The outer platform margin, traced from the anterior end, is more or less straight initially but is strongly constricted in front of the tongue; deflection of the inner margin is more evident in small specimens. The tongue is between one third and one half the total length (platform plus tongue) and tends to be very narrow and pointed. It may bear continuous transverse ridges, a carina, or developments intermediate between the two. The free blade measures about one third of the total unit length and bears six to nine sharp, oval (in cross section) denticles, which are longest and highest at midlength. Traced posteriorward, the fixed blade continues as a low fused carina which may extend, in a variable form, to the posterior tip. Due to the greater development of the outer platform, the carina tends to lie nearer to the inner margin. Aborally, a thick-lipped, slightly asymmetrical pit is situated a little anterior of the platform (minus tongue) mid-length. A sharp keel extends posteriorward, whilst anteriorward a relatively wide furrow can be traced on to the underside of the blade.

*Remarks:* The concept of *Po. l. mucronatus* is herein broadened to include forms both with and without a carina. This brings together specimens from the same fauna which are clearly related in their general robust character, platform ornament and in their cross-section. Ziegler and Klapper (1976) may have included only juvenile forms in their zeta morphotype; later growth stages have broader tongue developments, although the posterior constriction is still evident. Apart from the other members of the *Po. linguiformis* group, *Po. l. mucronatus* appears to lie closest to *Po. tuberculatus* Hinde (*q.v.*). Specimens referred to *Po. l. mucronatus* by Uyeno and Norris (1971), McGregor and Uyeno (1972) and by Telford (*cf.*, 1975) are not the same species.

*Polygnathus* aff. *porcillus* Stauffer

Plate 113, figs. 23, 25, 26

aff. 1940 *Polygnathus porcillus* n. sp.—Stauffer, p. 430, pl. 60, figs. 86–88.aff. 1970 *Polygnathus linguiformis linguiformis* Hinde—Bultynck, pp. 125–127, pl. 10, figs. 1, 2, 5.

*Description:* This specimen is characterized by an inturned posterior tip and an asymmetrically developed platform, the outer side of which is larger and extends further in both posterior and anterior directions. The platform margins bear short transverse ridges separated from the carina by adcarinal grooves. The anterior end of the platform lies perpendicular to the blade which is between one third and one half total unit length. A relatively large basal cavity is situated near the anterior end of the platform.

*Remarks:* This form differs from *Po. angustipennatus* s.l. in the asymmetry of the platform and in the posterior deflection. It is excluded from *Po. linguiformis* because of the pronounced carina extension, lack of a tongue development, the nature of the anterior platform margins, the general form of the blade and the relatively large basal cavity (cf. with juveniles of *Po. linguiformis*). Bultynck (1970, fig. 16, p. 122) considered *Po. angustipennatus* to have evolved from *Po. linguiformis* (during the mid Couvinian, Co2b) and figured specimens of the latter, which he did not exclude from being the first stage in such a development. The Plymouth specimen resembles these forms. The blade of *Po. porcillus* Stauffer is broken but the platform is very similar.

*Polygnathus pseudofolius* Wittekindt. Plate 108, figs. 1, 3–5, 7, 8 = 1966 *Polygnathus pseudofolius* n. sp.—Wittekindt, pp. 637–638, pl. 2, figs. 20–23.

*Polygnathus timorensis* Klapper, Philip and Jackson. Plate 112, figs. 13–15, 17, 18, 25, 28, 32, 35 = 1970 *Polygnathus timorensis* n. sp.—Klapper, Philip and Jackson, pp. 655–656, pl. 1, figs. 1–3, 7–10.

*Polygnathus tuberculatus* Hinde

Plate 113, figs. 1–4

1879 *Polygnathus tuberculatus* n. sp.—Hinde, p. 366, pl. 17, figs. 9, 10.. 1921 *Polygnathus tuberculatus* Hinde—Bryant, pp. 25–26, pl. 12, figs. 7–9.. 1934 *Polygnathus bryanti* n. sp.—Huddle, pp. 97–98, pl. 8, figs. 9, 10.?1956 *Polygnathus* sp. A—Hass, pp. 18–19, pl. 4, fig. 19.?1966 *Polygnathus bryanti* Huddle—Wittekindt, pp. 632–633, pl. 1, figs. 22–25.. 1975 *Polygnathus tuberculatus* Hinde—Gupta(a), pp. 116–117, pl. 2, fig. 1.. 1975 *Polygnathus tuberculatus* Hinde—Gupta(b), p. 163, pl. 1, fig. 3.

*Diagnosis:* A polygnathid with, in later growth stages, a thick, broad, strongly tuberculate platform, the anterior of which bears high subparallel ridges separated by deep adcarinal grooves.

*Remarks:* The specimens of *Po. tuberculatus* described and figured by Hinde (1879), Bryant (1921) and Huddle (1934) are relatively large and closely comparable with the Plymouth specimens. They are characterized by a carina which does not extend to the posterior tip but rather is developed only in the anterior two-thirds of the platform. The only earlier growth stages of this species which may have been figured previously are those of Wittekindt (1966), although this work did not include illustrations comparable with the holotype, and Ziegler and Klapper (*in* Ziegler *et al.* 1976) have recently referred Wittekindt's specimens to the eta morphotype of *Po. linguiformis* (= *Po. l. transversus*). The relationship of *Po. tuberculatus* to the former is uncertain, although it is noteworthy that the platform of *Po. tuberculatus* is reminiscent of the linguiform plan (a tongue is indicated but not well differentiated) and the basal configuration is identical to that of *Po. l. mucronatus*.

*Polygnathus* aff. *tuberculatus* Hinde. Plate 113, figs. 5, 8, 9, 13, 16, 21, 28 = ?1966 *Polygnathus bryanti* Huddle—Wittekindt, pp. 632–633, pl. 1, figs. 22–25.

*Remarks:* Included here are a number of specimens from Mount Wise with broad, flat platforms bearing transverse ridges and a variable rostral ridge development. In some, there is a relatively small tongue

development. These specimens resemble *Po. l. transversus*, the eta morphotype of Ziegler and Klapper (*in* Ziegler *et al.* 1976), but in the latter the outer platform margin is a regular curve throughout, whereas in the Plymouth specimens there is a change of curvature in the posterior platform, as is the case in *Po. bryanti* sensu Wittekindt. Also, the eta morphotype has a more distinct tongue.

A single large specimen from Plymouth (Plate 113, figs. 5, 8) differs from *Po. tuberculatus* in not bearing transverse ridges which converge toward the centre of the platform, and in lacking rostral ridges. Smaller specimens included here exhibit a variable platform development. In view of the variability shown by *Po. l. mucronatus* (*q.v.*), it seems probable that all these aforementioned forms may fall within the variability of *Po. tuberculatus*. The same may even be true of the eta morphotype of *Po. linguiformis* too.

#### *Polygnathus varcus* Stauffer group

*Remarks:* Klapper, Philip and Jackson (1970) defined the *Po. varcus* group as including polygnathids with narrow, parallel-sided platforms and relatively long blades. Within the group, species have been differentiated on the basis of the relative length and breadth of the platform, the nature of the anterior platform margins, the degree of platform ornament, and the position of the basal cavity. It should be noted however that representatives of the *varcus* group from Plymouth appear to display the following morphological changes during growth: platform ornament appears and may become most pronounced; the basal cavity migrates from a position at the blade/platform junction to a point posterior of this, and also becomes relatively smaller; there is a corresponding longitudinal growth of the platform and the blade consequently becomes relatively shorter; anterior trough margins may become flared. Platform symmetry, particularly that of the anterior trough margins, also varies between otherwise similar specimens, and it is the authors experience that this character does not provide a particularly useful criterion in the differentiation of members of the group. However, elements with unequal trough margins do not occur in *Po. varcus* faunas from Iowa and Minnesota (Klapper, written comm., 1975). Perhaps elements with asymmetric anterior platform developments were gained or lost through evolution of the *varcus* populations.

*Polygnathus varcus* Stauffer. Plate 109, fig. 29 = 1940 *Polygnathus varcus* n. sp.—Stauffer, p. 430, pl. 60, figs. 49, 53, 55.

*Polygnathus* aff. *variabilis* Bischoff and Ziegler. Plate 110, figs. 3, 5, 6, 8, 11, 15, 16, 19, 25 = aff. 1957 *Polygnathus?* *variabilis* n. sp.—Bischoff and Ziegler, pp. 99–100, pl. 18, figs. 8–17, 21–24; pl. 19, figs. 10, 11, 16, 17.

*Description:* The platform is mostly flat with straight, sub-parallel margins. The anterior inner platform is turned less abruptly toward the free blade and meets the latter further anteriorward than the outer margin. The outer platform tends to be broader than the inner, but both display variation in width and in ornament (absent or marginally nodose); there are shallow, relatively wide adcarinal grooves. Posteriorly, there is a linguiform tongue which is flexed both downward and inward; this is nearly as wide as the platform initially but thereafter may taper to a point (in narrow specimens) or may be broad and rounded terminally (in larger forms). The ornament of the tongue generally consists of curved transverse ridges which are convex posteriorward. The ridges may connect marginal nodes and may be interrupted by an incipient or discontinuous carina; short intercalated ridges and nodes occur at the margins.

The free blade is between one third and one half of the total unit length and is deepest at the downward arched anterior end. It bears seven to nine long, pointed and posteriorly inclined denticles which are highest and widest near the anterior end. Traced on to the platform, the denticles become increasingly fused and lie lower, but they nevertheless remain well above the level of the platform. In the smaller specimens, the denticles of the carina are relatively large and tend to persist further posteriorward, whereas the carina of the large forms diminishes progressively and disappears near the beginning of the tongue.

Aborally, a pit is situated a little behind the anterior end of the platform. This has wide and slightly raised margins which extend half the platform width on either side and posteriorward to platform midlength, at least. A sharp keel is developed in the posterior part of the unit while anterior of the pit, a furrow extends beneath the blade.

*Remarks:* Bischoff and Ziegler (1957) assigned *variabilis* to *Polygnathus* with question because of the incipient nature of the platform. Orr (1971, pl. 5, figs. 1–3) illustrated specimens with strong platform developments, but neither these nor the (illustrated) specimens from Germany (see also Wittekindt 1966,



pl. 3, figs. 11–14) bear the linguiform tongue characteristic of the Plymouth specimens; rather the carina is continuous to the posterior tip.

Associated with *Po. aff. variabilis* in the Gasworks Quarry (GW20) there is a lonchodiniform element (Plate 111, figs. 2–4) which bears thickened lateral margins with sharp nodes identical to the platform development in some specimens of the polygnathid. It seems probable that the two were associated naturally, perhaps within a species of the multielement *Parapolygnathus*.

*Polygnathus xylus* Stauffer. Plate 108, figs. 2, 9, 13, 21, 25 = 1940 *Polygnathus xylus* n. sp.—Stauffer, pp. 430–431, pl. 60, figs. 54, 66, 72–74.

*Polygnathus xylus ensensis* Ziegler and Klapper. Plate 108, figs. 2, 21, 25 = 1976 *Polygnathus xylus ensensis* n. subsp.—Ziegler *et al.*, pp. 125–127, pl. 3, figs. 4–9.

*Spathognathodus bidentatus* Bischoff and Ziegler. Plate 108, figs. 30, 31 = 1957 *Spathognathodus bidentatus* n. sp.—Bischoff and Ziegler, pp. 114–115, pl. 6, figs. 8, 13.

*Spathognathodus brevis* Bischoff and Ziegler. Plate 108, figs. 22–24, 27 = 1957 *Spathognathodus brevis* n. sp.—Bischoff and Ziegler, pp. 116–117, pl. 19, figs. 24, 27–29.

*Spathognathodus planus* Bischoff and Ziegler. Plate 111, figs. 9, 13, 17 = 1957 *Spathognathodus planus* n. sp.—Bischoff and Ziegler, p. 117, pl. 19, figs. 34, 35.

*Remarks*: This element displays variation in the degree of arching and lateral flexing, and in the regularity of the denticulation. The denticle (cusp) immediately above the basal cavity is generally slightly larger than those adjacent to it. *Bryantodus versus* Stauffer (1940) is very similar but bears a more conspicuous cusp.

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